

HABITAT REQUIREMENTS FOR CHESAPEAKE BAY LIVING RESOURCES



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Second Edition

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EXECUTIVE SUMMARY

"Habitats are the places where plants and animals live, where they feed, find shelter, and reproduce."

CHAPTER 1

The 1987 Chesapeake Bay Agreement committed the signatories to develop "guidelines for the protection of habitats and water quality conditions necessary to support the living resources found in the Chesapeake Bay system, and to use these guidelines in the implementation of water quality and habitat protection programs." This report is a comprehensive revision of earlier guidelines: *Habitat Requirements for Chesapeake Bay Living Resources*, adopted by the Chesapeake Executive Council in 1988.

A primary purpose of this revision is to provide a technical basis for development of habitat and water quality restoration goals. Further, as a comprehensive and up-to-date summary of a large amount of scientific and technical literature, it will be a valuable reference for technical environmental staff in public agencies and the private sector, for researchers, and for students.

OVERVIEW

This document was developed under the direction of the Habitat Objectives Workgroup of the Chesapeake Bay Program's Living Resources Subcommittee. Its completion was made possible by the generous assistance of numerous Bay-area scientists, the Bay Program's Scientific and Technical Advisory Committee, the Chesapeake Research Consortium, Inc., and a grant from the National Oceanic and Atmospheric Administration, Office of Ocean and Coastal Resource Management.

Information on the life histories, ecological roles, habitat requirements, and special concerns for 31 "target species", compiled and interpreted from extensive literature by recognized experts, is presented in 20 chapters. The target species, selected by the former Living Resources Task Force as a step in developing the first edition, were chosen for their commercial, recreational, and ecological importance. The Task Force intended that the target species, both directly and through their ecological associations, would represent all major trophic levels and aquatic habitat types in Chesapeake Bay. Two additional chapters are syntheses of information on contaminant effects on the target species. The 47 maps in the Appendix display recent information, compiled under the supervision of the chapter authors, on the distributions of the target species and their habitats.

Each chapter is summarized below, with a discussion of known habitat requirements and ecological roles for each species. The essential needs of each species are highlighted. Graphics have been provided to give a broad

overview of: (1) seasonal occurrence of target species in the Bay by life stage, (2) a ranking of identified problems for target species, (3) minimum water quality requirements, and (4) toxicity of selected contaminants.

Although more than 2000 references are cited in this volume, habitat needs could not be completely defined for all of the target species. The authors have identified where important information is lacking and have made appropriate recommendations for research and monitoring. Research is needed to better define the habitat requirements of the Bay's living resources, and to understand relationships between habitat quality and the abundance and health of species and communities.

The authors and editors of this report have put considerable effort into summarizing information in tables, maps, and the species summaries and graphics presented below. However, these aids are intended to be illustrative rather than definitive, and readers are cautioned that the summaries do not present the complete picture of habitat requirements for any of the species or habitat variables. The individual chapters and the primary references should be consulted before attempting to use the habitat requirements information in any important context.

SPECIES SUMMARIES

Submerged aquatic vegetation

Fifteen species of SAV commonly occur in the Chesapeake Bay and its tidal tributaries. The five species in this report include widgeon grass, eelgrass, sago pondweed, wild celery, and redhead grass. They represent species

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which inhabit the full range of salinity concentrations that occur in the Bay: tidal fresh, oligohaline, mesohaline, and polyhaline waters. These plants play an important ecological role by providing habitat for small forage fish, shellfish, benthic epifaunal and infaunal assemblages, and as food for waterfowl. The Baywide decline in SAV distribution and abundance is considered to be a primary cause of the decline in waterfowl populations that rely on aquatic habitats for food.

“SAV provides habitat for fish and wildlife, food for waterfowl, absorbs nutrients...and produces dissolved oxygen.”

CHAPTER 2

Recommendations for SAV:

- * Increase water clarity*

Eastern oyster

The eastern oyster is well adapted to an estuarine environment. It tolerates wide fluctuations in temperature, salinity, suspended sediments, and has a tremendous capacity to reproduce if habitat conditions and brood stock are adequate. Oysters filter water for food, improving water clarity conditions for SAV and other species. Baywide harvests have declined drastically over the past century. Since the 1960's, parasitic diseases have had major impacts on Bay oyster populations.

Recommendations for eastern oyster:

- * Restore SAV beds*
- * Enhance seed & cultch supply*
- * Research*
 - larval biology*
 - feeding and nutrition*
 - disease*
 - pollutant impacts*

Soft shell clam

Soft shell clams, widely distributed marine and estuarine bivalves, can reproduce rapidly under optimum conditions. This species is most abundant in mesohaline areas of the Bay with coarse or sandy substrate. Predators largely limit survival of the species in polyhaline waters and in mud substrates. Principal ecological roles performed by the species are filtering the water column, providing shell substrate for fouling invertebrates, and

serving as prey (all life stages) for a wide assortment of animals.

Recommendations for soft shell clam:

- * Maintain adult reserve areas*
- * Protect oyster beds and SAV from clam dredging*
- * Contaminants of concern*
 - oil spills*
 - copper*

Hard clam

The hard clam, distributed in marine and estuarine waters along the Atlantic and Gulf Coasts, is limited to salinities greater than 12 ppt and is most abundant in salinities greater than 18 ppt. In Chesapeake Bay, it is generally restricted to Pocomoke and Tangier Sounds and subestuarine river systems in Virginia greater than 5 m deep; highest densities exist in the lower York and James Rivers. Hard clams are important suspension-feeders. The Bay supports a modest fishery for hard clams.

Recommendations for hard clam:

- * Research*
 - early life history*
 - larval settlement & recruitment*
 - toxics*

Blue crab

The blue crab population presumably supports the largest harvests of any fishery species (except Atlantic menhaden) in the Bay, representing half of the U.S. blue crab harvest. The species is tolerant of fluctuating environmental conditions and is ubiquitous during its peak summer abundance period. The blue crab is a major predator and omnivore within the Bay and all life stages serve as an abundant source of prey to other species. The Bay population is controlled by the return of postlarval crabs from coastal waters. Crabs use all habitats in the Bay, preferring near shore and creek waters, SAV beds, and deeper water in winter.

“Blue crabs utilize all habitats in the Bay, from the deepest to the water's edge and from the most saline to fresh water.”

CHAPTER 6

Recommendations for the blue crab:

- * Raise DO to 3.0 mgL^{-1}
- * Protect shallow water habitats
- * Preserve SAV
- * Reduce toxics
- * Monitor populations
- * Research

*seasonal habitat by age
population dynamics*

Atlantic menhaden

The Atlantic menhaden, one of the most abundant species in estuarine and coastal Atlantic waters, is the second most-harvested fish in the United States. Menhaden are processed into oil, protein meal, and solubles, and used extensively as bait for commercial and recreational fishing. The Atlantic menhaden, unlike most shad and herring, is a coastal ocean spawner, although minor spawns occur in the lower Bay. Menhaden are major consumers of plankton and detritus, consuming zooplankton as very young larvae and maturing to filter-feed on phytoplankton and detritus. Menhaden are important prey to many predatory fish and birds, thus forming an important link in the overall Chesapeake Bay and coastal shelf food webs.

"During summer in the Chesapeake Bay...acres of these silvery fish are frequently seen dappling the water's surface."

CHAPTER 7

Recommendations for Atlantic menhaden:

- * Increase DO in small tributaries
- * Research
- ecological role as filtering and recycling agents*

Bay anchovy

The bay anchovy, a small, schooling species, is the most abundant and wide-ranging finfish in the Chesapeake Bay. Occurring throughout the year, it is a major consumer of zooplankton and is, at all life stages, a major food of predatory fish, terns, and jellyfish making it a key species in the Bay's food web.

Recommendations for the Anchovy:

- * Increase DO

** Research*

*toxics
plankton foods
biomass consumed
population dynamics*

American shad and hickory shad

American shad and hickory shad are large anadromous herring of the eastern seaboard with hickory shad being more southern in distribution. Both spawn in the Bay during spring, generally peaking in April for American shad and May for hickory shad. American shad and hickory shad are principally zooplankton feeders and, in turn, are preyed upon (eggs, larvae, and juvenile stages) by other predatory fish, thus serving as a trophic link between plankton and piscivores in coastal and estuarine waters. In the late 19th century, American shad supported major fisheries along the Atlantic seaboard, whereas hickory shad were of minor importance as a food fish. Spawning stocks in the Bay for both species are now at very low levels in all spawning tributaries. A moratorium on fisheries for both species has been in effect in Maryland for at least 10 years.

Recommendations for shad:

- * Restock and restore populations
- * Provide passage
- * Maintain monitoring
- * Investigate further harvest restrictions
- * Research
- habitat in spawning reaches
acid rain*

Alewife and blueback herring

These two species are relatively small anadromous herring occurring virtually in all of the Bay's tributaries, although abundance is very much depressed. Both species feed principally on zooplankton, small insects, fish eggs, and the like, serving as an important trophic link to estuarine and coastal piscivores, and to some mammals, amphibians and aquatic birds. Larval forms and eggs of these species also serve as prey for small fish and invertebrates. These two species, often known as river herring, historically supported a fairly significant fishery.

Recommendations for herring:

- * Manage stocks
- * Provide passage
- * Improve spawning habitat
- * Reduce exposure to low pH

Spot

Spot is an abundant marine and estuarine bottom foraging species. They occupy all areas of the Bay except in winter when they migrate to coastal waters or concentrate in deep-water refuges in the Bay. Spot are tolerant of a range of environmental conditions, generally preferring brack-

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ish to saline waters above mud substrates in the Bay, although they occur ubiquitously throughout all Bay depths. They are short-lived coastal spawners with excellent reproductive capacity; major predators of shallow benthic invertebrate communities in the Bay; and important prey to a host of predatory fish. The larvae consume zooplankton. Spot support a modest commercial fishery and are frequently (often incidentally) taken by sport fishermen in summer and fall.

"...spot is one of the major regulators of benthic invertebrate communities in the Chesapeake..."

CHAPTER 11

Recommendations for Spot:

** Research*

*population dynamics
stock-recruitment
water quality impact*

White perch

The white perch is a semi-anadromous estuarine fish occurring in all major tributaries of the Bay, with each river system apparently maintaining its own separate population. The peak spawning period is April-May. Juvenile white perch feed largely on zooplankton, larvae, insects and amphipods; adults are piscivores but also prey on benthos. The species occupies an important trophic link between small invertebrates and higher predators, primarily piscivorous predators. Although commercial landings (largely by-catch of the striped bass commercial harvest) of white perch have generally declined from sizeable harvests (1-2 million pounds) in the 1960's and early 1970's, the population does not appear to have experienced overexploitation. It supports an important sport fishery.

"The inshore zones of estuaries and creeks...are the primary nursery areas for juvenile white perch..."

CHAPTER 12

Recommendations for white perch:

** Increase DO*

** Protect deep-water refugia from dredge spoil*

** Research population dynamics*

Striped Bass

The striped bass ("rockfish") is a large anadromous fish which spawns in Chesapeake Bay tributaries in April and May in tidal fresh water above the salt wedge. The Bay is the principal spawning and nursery area for the Atlantic coast striped bass stock. Striped bass are voracious predators and grow rapidly. Larvae feed on a variety of zooplankton and juveniles feed on fish larvae, insects, worms, mysids, and amphipods. Adults are piscivorous, consuming bay anchovy, spot, menhaden, herring, shad, white perch, and yellow perch. Striped bass eggs, larvae, and juveniles serve as important prey for higher predators. Striped bass previously supported a major fishery throughout the Atlantic Coast states, although declining populations have forced restrictive harvest regulations in Chesapeake Bay.

Recommendations for striped bass:

** Increase DO*

** Reduce turbidity*

** Continue conservative management*

** Improve water quality in spawning habitats*

Yellow perch

The yellow perch is a freshwater species that has adapted to a semi-anadromous existence in the Bay where it occurs in all major tributaries. Yellow perch spawn in mid-February and March. Adults remain in their natal river systems. Yellow perch link zooplankton and benthic communities to higher predatory fish and birds. Larvae feed on zooplankton, juveniles progressively feed on benthic fauna, and even larval yellow perch, and adults are largely piscivorous on anchovies, killifish, and silversides. The Bay once sustained a vigorous yellow perch fishery, with harvests over one million pounds annually at the turn of the century. The annual catch has declined to about 40,000 pounds. The Bay's yellow perch population has declined significantly over the past several decades. There has been an absence of spawning in several lower Western Shore tributaries.

Recommendations for yellow perch:

** Protect stocks*

** Research*

*stocks and recruitment
acid rain*

Wood duck

The wood duck is generally confined to forested regions and nests in tree cavities. Wood ducks are present in the

Chesapeake Bay region in all but the coldest winter months. They use a variety of freshwater wetland habitats for migration, breeding, brood rearing, molting, and roosting. Wood ducks are omnivores, consuming a variety of vegetation as well as invertebrates, fish, amphibians, and crustaceans. Wood ducks provide a valuable link in wooded wetlands between plants and invertebrates and higher predators, particularly great horned owl, mink, raccoon, and fox.

Recommendations for the wood duck:

- * *Protect forested & riparian habitat*
- * *Maintain natural hydrology*
- * *Manage timber harvest*

Black duck

The black duck is a dabbling duck which inhabits inland and emergent wetlands throughout Chesapeake Bay to migrate, breed, and winter, principally around the mid-Eastern Shore and Western Shore of Virginia. Black ducks are omnivores, consuming small fish, mollusks, and a variety of vegetation, including SAV and agricultural crops. SAV is extremely important to black duck nesting and brood rearing in brackish and salt marshes. Black ducks provide a valuable link between herbaceous plants and invertebrates and higher predators, including bald eagles, foxes, and great horned owls. During the 1950's, a large portion (20%) of the continental population of black ducks wintered on Chesapeake Bay. Up to 224,000 birds used the Bay then, whereas now the annual wintering population averages about 30,000.

Recommendations for the black duck:

- * *Expand refuges*
- * *Restore SAV*
- * *Research*
 - hybridization*
 - reliance on cereal grain*
 - habitats on regulated shooting areas*

Canvasback

Canvasbacks are diving ducks of inland and coastal habitats. They favor shoal-water habitats with plentiful SAV or small bivalves. Canvasbacks use the Bay for winter refuge from about December through March. Canvasbacks are principally herbivores; they feed on SAV, preferring sago pondweed and wild celery. They represent a link between plants and certain higher predators such as bald eagles. The decline of SAV on the Bay has led canvasbacks to rely heavily on Baltic clams. Chesapeake Bay was historically the single most important wintering ground for canvasbacks in North America, wintering over 250,000 birds. Before the turn of the century, canvasbacks supported a vigorous commercial market, which decimated populations. Today about 50,000 annually winter here.

Recommendations for the canvasback:

- * *Restore SAV*
- * *Establish open water sanctuaries*
- * *Research*
 - ecology*
 - nutrients*
 - energetic relationships*

Redhead

Redheads are diving ducks closely related to the canvasback. They are sporadic fall and spring migrants to the Bay, generally wintering farther south in marine water or hypersaline lagoons. The redhead feeds almost exclusively on SAV and has nearly abandoned the Bay because of SAV declines. In the mid 1950's, about 70,000 redheads wintered in the Bay, whereas now about 2,000 winter here.

Recommendations for the Redhead:

- * *Restore SAV*
- * *Research*
 - nutrient cycling*
 - contaminants*
 - energetic relationships*

Colonial wading birds

Six species of colonial nesting wading birds - the great blue heron, great egret, snowy egret, little blue heron, green-backed heron, and black-crowned night heron - are prominent avian residents of the Chesapeake Bay region. Colonial wading birds are extremely predaceous, feeding mostly on small fish, amphibians, crustaceans, and aquatic insects in a variety of aquatic habitats. All six species breed in the Chesapeake Bay and migrate south in the winter, although small numbers of great blue herons and black-crowned night herons are year-round residents. Most birds begin to arrive on the Chesapeake breeding grounds from mid-March to mid-June. Nesting habitat common to all six species includes the presence of woody vegetation and isolation from human and animal predators. Great blue herons prefer tall trees (7-10 m), either live or dead, inhabit both hardwoods and evergreens, and avoid areas with human activity. The largest colonies are found in the upper reaches of the Bay in woodland swamps adjacent to large tributaries. Black-crowned night herons, great and snowy egrets, and little blue herons tend to nest on islands with shrubby vegetation, often in mixed-species colonies. Green-backed herons are the most solitary nesters of the group, but at times can be found with other herons and egrets. They use both shrubs and small trees and can often be found nesting on duck blinds. Populations of these species appear to be stable, with the exception of the little blue heron, which has declined. Numbers of great blue herons may actually be increasing, although higher population counts may be attributable to expanded inventory areas. The Bay region contains the five largest Atlantic Coast colonies of great blue herons.

***"...herons and egrets
are top-level
predators in the
Chesapeake Bay
system."***

CHAPTER 19

Recommendations for colonial wading birds:

- * Improve water quality for prey*
- * Protect nesting and foraging sites and islands*
- * Research foraging and nesting patterns*

Osprey

Ospreys feed almost exclusively on live fish, and are often referred to as fish-hawks. Ospreys are distributed throughout the tidal Chesapeake Bay, from late February through September, spending the winter in South America. Nesting occurs primarily along the Bay shorelines and the wide shallow portions of its tributaries, on navigation markers, utility poles, nest platforms, hummocks, duckblinds, and dead trees. The osprey's position as a primary consumer at the top of the aquatic food chain proved hazardous in the 1950's through the early 1970's when organochlorine pesticides (DDT) adversely affected reproductive success and caused a serious population decline. The banning of some persistent pesticides during the 1970's has enabled Chesapeake osprey populations to grow during the 1980's to an estimated 2,000 pairs.

Recommendations for osprey:

- * Improve water quality for prey*
- * Maintain availability of nest sites*
- * Monitor organochlorine contaminants*

Bald eagle

Bald eagles are predators known for their fish-eating habits. They are also opportunistic scavengers, consuming a variety of species. In Chesapeake Bay, adult eagles generally remain in their nesting territories throughout the year. They nest along the undeveloped shorelines of the Bay, usually within 1 km of the water. Nesting densities are greatest along the Potomac and Rappahannock Rivers and in Dorchester County, Maryland. The habitat required by eagles can be described as shoreline with minimal human disturbance, having large old-growth forest stands with large (50 cm diameter) trees adjacent to undisturbed waters that harbor abundant fish and waterfowl. Chesapeake Bay may once have provided habitat for as many as 3,000 pairs of bald eagles, but due to habitat destruction, shooting, and DDT, the population declined to a low

of 80 to 90 pairs by 1970. Following a ban of DDT, the population has increased to 185 nesting pairs in Maryland and Virginia during 1989. The greatest threat to the Chesapeake eagle today is the loss of shoreline forests that they need for nesting, roosting, and perching. These forests are rapidly being developed for human use.

***"The fate of the eagle
on the Chesapeake
Bay will mirror the
fate of the shoreline
forests..."***

CHAPTER 21

Recommendations for the bald eagle:

- * Protect nest sites*
- * Protect shoreline forests*
- * Research current pesticide risks*

Effects of contaminants on fish and shellfish

This chapter summarizes information on contaminant effects on the target species of fish and shellfish. The Chesapeake Bay Program has identified a list of "Toxics of Concern" comprised of toxic substances that by their toxicity, persistence, or widespread use, present a threat or potential threat to humans and living resources in the Bay region. The Toxics of Concern list was used to select toxicants for emphasis in the synthesis chapter.

A summary of chemical-specific toxicity, tested in the laboratory on aquatic target species, shows the varying sensitivities species have to different contaminants. Certain contaminants clearly could pose serious threats to exposed target species. They include aldrin and dieldrin (oyster and spot), cadmium (striped bass), chlordane (oyster, yellow perch), lead (American shad), mercury (oyster, hard clam, blue crab, spot, striped bass, and white perch), copper (oyster, soft shell clam, and hard clam), PCB (oyster, spot), toxaphene (oyster, spot, striped bass, and yellow perch), and tributyltin (oyster, hard clam, menhaden, hickory shad, and striped bass).

Recommendations:

- * Minimize loads of toxic contaminants*
- * Identify affected areas*
- * Synthesize information loads, fate, and effects*

Effects of contaminants on birds

Apart from isolated examples of the possible continuing effects of past contaminant exposure, there is little evidence that contaminants in Chesapeake Bay currently pose a serious hazard to birds from direct toxicity. Organochlorine pollutants such as dieldrin caused deaths of birds in the Chesapeake Bay in the past. Reproduction of birds was impaired by DDE, which is a metabolite of the pesticide DDT. Lead poisoning, the result of ingestion of spent lead shot used by hunters, also may have reduced survival. The banning of the most harmful organochlorine pesticides and the replacement of lead shot with steel shot have reduced mortality and reproductive problems.

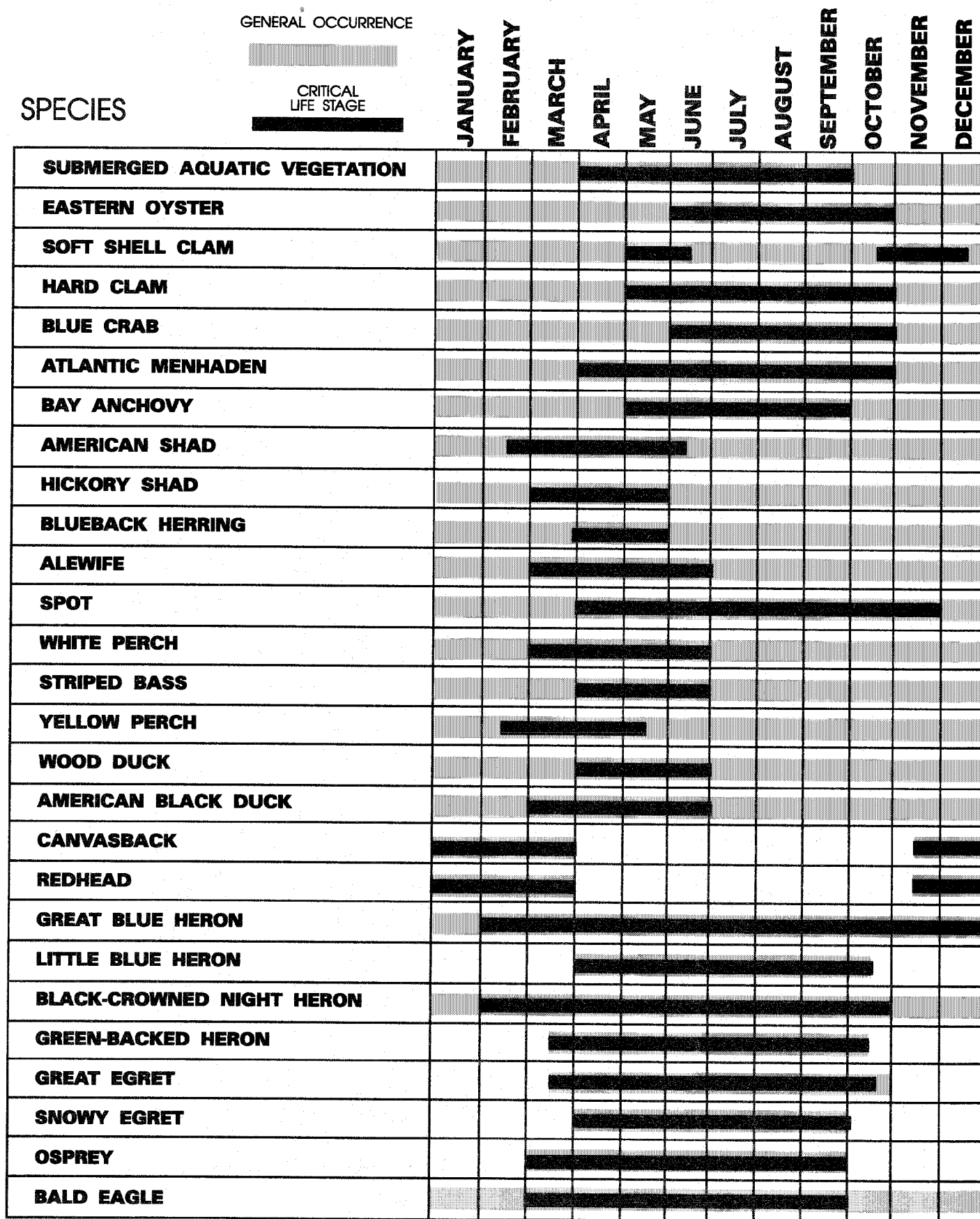
The major classes of contaminants of concern are organochlorines, heavy metals, oil, cholinesterase inhibiting pesticides, and herbicides. Organochlorines include

polychlorinated biphenyls (PCB) and pesticides such as dieldrin, kepone, and DDT and its metabolite DDE. Organophosphorus and carbamate pesticides, such as abate and carbofuran, are cholinesterase inhibitors. The direct effects of these contaminants on birds is probably less important than the indirect effects on aquatic habitat by excess nutrients, suspended sediments, and possibly herbicides. The loss of SAV in the Bay is perhaps the best example of an indirect effect of pollutants on waterfowl abundance and distribution.

Recommendations:

- * Monitor for contaminant effects*
- * Identify contaminants of concern*
- * Reduce nutrient loads*
- * Restore SAV*

SEASONAL OCCURRENCE OF TARGET SPECIES ON CHESAPEAKE BAY



IDENTIFIED PROBLEMS FOR TARGET SPECIES IN THE CHESAPEAKE BAY

	DO	NUTRIENTS	LIGHT ATTENUATION	SUSPENDED SOLIDS	PH	CONTAMINANTS	PETROLEUM	DISEASES	OVERHARVEST	SPAWNING BLOCKAGES	LAND USE/DEVELOPMENT	LOSS OF SAV	HUMAN DISTURBANCE	OTHER
SAV		●	●	●		◐				○				◐ ^{1,2}
OYSTER	○	○		●		◐	◐	●	●		○			● ³
SOFT SHELL CLAM	○	○				○	◐	○	○					○ ⁴
HARD CLAM	○	◐		◐		◐	◐		○		○			● ⁵
BLUE CRAB	●					◐			○		○	○		○ ⁶
MENHADEN	◐						◐	○						
BAY ANCHOVY	◐					○								◐ ⁷
SHAD	○			◐	●	◐			●	●	○			
HERRING	○			◐	●	◐			●	●	○			
SPOT	◐					○								
WHITE PERCH	◐			○		◐			○					
STRIPED BASS	◐			○	●	●			●					◐ ⁴
YELLOW PERCH	○	○		●	●	◐			◐	●	○			○ ⁶
WOOD DUCK						○	○		○		◐		○	○ ⁸
BLACK DUCK						○	○	○	◐		◐	●	◐	○ ^{9,10}
CANVASBACK						○	○		◐			●	○	○ ⁹
REDHEAD						○	○		◐			●	○	
WADING BIRDS						○	◐				◐	○	○	
OSPREY						◐	○				◐		○	
BALD EAGLE						◐	○				●		●	● ⁶

LEGEND

- KNOWN TO HAVE MAJOR IMPACT ON SPECIES OR HABITAT
- ◐ KNOWN TO HAVE LOCAL IMPACTS ON SPECIES OR HABITAT

- POTENTIAL PROBLEM OR UNCERTAIN IMPACT
- NOT BELIEVED TO BE A PROBLEM OR NOT RELEVANT TO THE SPECIES

OTHER

1. BOAT DAMAGE
2. FORAGING
3. LACK OF SUBSTRATE
4. HIGH TEMPERATURE
5. INTRINSIC LOW RATE OF RECRUITMENT

6. LOSS OF SHORELINE HABITAT
7. ENTRAINMENT IN INDUSTRIAL WATER INTAKES
8. LEAD SHOT
9. ARTIFICIAL FEEDING
10. HYBRIDIZATION

Summary of reported water quality requirements for aquatic target species in Chesapeake Bay. Consult chapters for discussion of values. Water quality levels for SAV and prey species will also benefit avian target species. Parameters: DO = dissolved oxygen; DIN = dissolved inorganic nitrogen; DIP =

Species/Parameter	DO mgL ⁻¹	DIN mgL ⁻¹	DIP mgL ⁻¹	K _d m ⁻¹	Secchi m
SAV Tidal Fresh			< 0.02	< 2	> 0.8
SAV Oligohaline			< 0.02	< 2	> 0.8
SAV Mesohaline		< 0.15	< 0.01	< 1.5	> 1.0
SAV Polyhaline		< 0.15	< 0.02	< 1.5	> 1.0
Eastern oyster	> 1.0				
Soft shell Clam					
Hard Clam	> 5.0				
Blue Crab	> 3.0				
Atlantic Menhaden	(1.1=m)				
Bay Anchovy	> 3.0				
American Shad (Hickory shad req. assumed to be similar)	> 5.0				
Alewife	> 5.0 (E,L) > 3.6 (J,A)				
Blueback Herring	> 5.0 (L,A) > 3.6 (J)				
Spot	> 2.0				
White Perch	> 5.0				
Striped Bass	> 5.0				
Yellow Perch	> 5.0 (J,A)				

dissolved inorganic phosphorus; K_d = light attenuation; Secchi = Secchi disc depth; TSS = total suspended solids. Life stage: E = eggs; L = larvae; J = juvenile; A = adult. Blank boxes indicate insufficient data available or not applicable to the species; m = mortality.

TSS mgL ⁻¹	Chlorophyll <i>a</i> mgL ⁻¹	Temperature °C	pH	Salinity ppt
< 15	< 15			
< 15	< 15			
< 15	< 15			
< 15	< 15			
(250=m) (E,L)		19-32 (E,L), 7-32 (A)	6.75-8.75 (E,L)	12-27
		10-20 (E), 2-34 (A)		> 8
< 750 (E) < 250 (L) < 44 (A)		7.5-32.5 (E) 12.5-33.0 (L) 1.0-34.0 (A)	7.0-8.75 (E) 7.5-8.50 (L)	20-35 (E) 17-35 (L) > 15 (A)
		5-39	> 7	> 20 (L), 0-30 (A)
				5-10 (J), 3.5 (A)
		13-30 (E), 15-30 (L) 10-30 (J), 8-32 (A)		4-20 (E), 0-15 (L) 9-30 (J,A)
< 1000 (E) < 100 (L, J,A)		13.0-26.0 (E) 15.5-26.1 (L) 15.6-23.9 (J) 10-30 (A)	> 6.0 (E) > 6.7 (L)	0-15 (E) 0-30 (J,A)
< 1000 (E)		11-28 (E), 8-31 (L) 10-28 (J),	5.0-8.5 (E) 5.5-8.5 (L)	0-2 (E), 0-3 (L) 0-5 (J), 0-30 (A)
< 1000 (E) < 500 (L) (830 L=m)		14-26 (E), 14-28 (L) 10-30 (J)	5.7-8.5 (E) 6.2-8.5 (L)	0-1 (E), 0-2 (J), 0-35 (A)
(88=m)		6-25		
< 100 (E) < 500 (L, J,A)		12-20 (E,L) 10-30 (J,A)	6.5-8.5 (E,L) 7-9 (J)	0-2 (E,L), 0-3 (J) 5-18 (A)
< 1000 (E) < 100 (L)		12-23 (E,L) 10-27 (J) 20-22 (A)	7-9.5 (E) 7-8.5 (L) 7-9.0 (J)	0.5-10.0 (E) 1.0-10.5 (L) 0-16 (J)
< 1000 (E) < 500 (L)		7-20 (E) 10-30 (L,J) 6-30 (A)	6.0-8.5	0-2 (E,L) 0-5 (J) 0-13 (A)

Toxics of Concern for Target Species in Chesapeake Bay. Data are from Chapter 22, this volume, EFFECTS OF CONTAMINANTS ON FISH AND SHELLFISH and represent geometric means of literature values for acute toxicity and chronic or sublethal toxicity to target species, giving a

	Acute toxicity (µg/l) / Chronic or Sublethal Toxicity (µg/l)			
Contaminants/Species	Eastern Oyster	Soft Shell Clam	Hard Clam	Blue Crab
Aldrin (insecticide)	15/0.1		ND/2025	23/ND
Arsenic (metalloid)	7500/ND			
Atrazine (herbicide)	> 30,000/ > 10,000			
Cadmium (heavy metal)	2579/39	1672/ND		1272/50
Chlordane (insecticide)	8/6			ND/353
Chromium VI (heavy metal)	10,300 /ND	57000/ND		75784 /1500
Copper (heavy metal)	38/50	58/ND	22/25	
Dieldrin (insecticide)	67/13			240/ND
Dimilin	> 130,000		> 1 x 10 ⁶	260
Fenvalerate (insecticide)	> 1000 /ND			
Lead (heavy metal)	2450/ND	2700/ND	780/ND	
Mercury (heavy metal)	8/12	400/ND	20/14	ND/10
PCB (polychlorinatedbiphenyl)	10/13.9			
Permethrin (insecticide)	> 1000 /ND			
Toxaphene (insecticide)	23/40		< 250 /1120	180/ND
Tributyltin (antifoulant)	1.5/0.7		0.05/0.08	
Zinc (heavy metal)	263/200	6328/ND	190/ND	

^a Toxicity tests with striped bass and white perch were conducted in fresh water.

^b Toxicity tests with striped bass and white perch were conducted in saline water.

relative indication of potential effect. End points and exposure times varied. Life stages were pooled for calculating means. ND = no data available.

Based on Geometric Means of Literature Values

Atlantic Menhaden	Hickory Shad	American Shad	Spot	Striped Bass	White Perch	Yellow Perch
			3.2/1.4	8 ^b /ND	102/ND	
				20,248 ^a /ND	750 ^a /ND	
			8500/ND			
			387/316	8.3 ^a ,38 ^b /2	1712 ^a /ND	
				12/ND		10/ND
			2700/ND	16,370 ^a 58,000 ^b /ND	10,300 ^a /100	36,300 /ND
610/ND			212/ND	54 ^a /ND	309/50	
				20/ND		
						> 50,000
		< 10/ND			2450/ND	
			36/ND	90 ^a /5	8.5/10	
			0.5/1.6			240/ND
			1.7/.03	5 ^a ,5.8 ^b /ND		12/ND
4.5/ND	ND/9			< 2.0/25		
		< 30/ND	3800/ND	322 ^a /430	2105/ND	

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INTRODUCTION

Stephen J. Jordan, Joseph A. Mihursky and Steven L. Funderburk



Declines in populations of important Chesapeake Bay species have focused attention on human influences on habitats, and on the potential and mechanisms for protecting and restoring their integrity. This report is a compilation and partial synthesis of a large body of information about habitats and species habitat needs in Chesapeake Bay - an accomplishment that will advance general understanding of the relationships between the Bay's living resources and their habitats.

Background

The Chesapeake Bay Program's goal for living resources is to "provide for the restoration and protection of the living resources, their habitats, and ecological relationships". The first commitment toward this goal is to "develop and adopt guidelines for the protection of water quality and habitat conditions necessary to support the living resources found in the Chesapeake Bay system, and to use these guidelines in the implementation of water quality and habitat protection programs." This commitment was fulfilled through the adoption by the Chesapeake Executive Council of the first (1988) edition of *Habitat Requirements for Chesapeake Bay Living Resources*.² Although a useful step toward defining necessary habitat conditions for target species, and calling attention to needs for habitat restoration, the first edition was somewhat limited in coverage and literature support. It was recognized that more comprehensive guidelines would be required to provide the information base necessary for effective use in water quality and habitat restoration programs. Therefore, the Habitat Objectives Workgroup of the Chesapeake Bay Program's Living Resources Subcommittee undertook this revision of the first edition.

On the advice of the Chesapeake Bay Scientific and Technical Advisory Committee's Living Resources Workgroup, experts from several research institutions and resource management agencies were recruited to synthesize the

Habitats are the places where plants and animals live, where they feed, find shelter, and reproduce. Habitats may be relatively small, well-defined areas (the nesting and feeding area of an osprey pair, for example), or may encompass large regions (for some migratory fish, the northwest Atlantic coastal plain and its estuaries). Habitats vary in time, in response to seasonal and long term changes in temperature, salinity, and human impacts, among many other variables. If the changes are too severe, the habitat may become unsuitable for a species, resulting in a local or regional population decline.

best available information on selected ("target") species and to identify the most limiting environmental factors for each of the species. The Chesapeake Research Consortium, Inc., played an important role in coordinating and promoting this complex project.

Purpose

How should this document be used, and by whom? This report will be a valuable reference for technical environmental staff in public agencies and the private sector, for researchers, and for students. It is a reasonably complete and up-to-date summary of a large amount of literature and expert experience on the target species, their habitat needs, life histories, and ecological relationships, as well as gaps in our knowledge of these matters. Following are some comments about the report's values, weaknesses, content, and organization, along with suggestions and caveats about its use.

This volume is an attempt to bridge physical, chemical, and biological elements that are known or believed to be important for the selected species based upon available data and information. Authors were asked to look beyond survival thresholds to define habitat conditions needed for the growth, reproduction, and natural behavior representative of healthy populations. Naturally, there are variations in emphasis between chapters, reflecting both

INTRODUCTION

the availability of information and the special concerns unique to species or taxonomic groups.

The authors and editors have spent considerable effort on summarizing information in tables, maps, and the Executive Summary, but these aids do not stand alone. Users are cautioned not to apply the summary information without reference to detailed information in the species chapters and the primary references cited in them. Each chapter was edited for readability and overall consistency of style; the editors are responsible for any failures on these points.

In compiling comprehensive information on the habitat requirements of 31 target species representing all major trophic levels, and accounting for the most important interactions among the species, their predators, prey, and habitats, we have begun to assemble a descriptive model of the Chesapeake Bay ecosystem. This model is both too simplistic for predictive purposes and too detailed for the regional management planning that it should serve, however. The model needs to be extended in two directions. First, we can achieve greater predictive power by specifying and quantifying the processes that couple species to each other and to their habitats in space and time. Second, we can provide managers and planners with tools for setting goals, evaluating options, and measuring progress by synthesizing the habitat requirements across the spectrum of species and integrating them over regions, depths and seasons. Both of these directions have been recognized by the Chesapeake Bay Program, and the next logical steps are being taken.

In the first instance, a team of managers, scientists, and reviewers has been assembled to advance and coordinate the development of simulation models of Chesapeake Bay ecosystem processes. These models, directed ultimately towards an integrated ecosystem model, eventually will provide quantitative answers to difficult habitat questions that could not be answered by the present authors (for example, what are the indirect effects of excess nutrients on animals at the top of the aquatic food chain?).

In the second instance, significant progress has been made in synthesizing the information compiled in this volume. Two reports have been drafted and are under review that provide the multi-species synthesis and integration necessary for regional planning purposes: (1) *Chesapeake Bay Dissolved Oxygen Restoration Goals*³; and (2) *Chesapeake Bay Submerged Aquatic Vegetation Habitat and Restoration Goals: A Technical Synthesis*.¹ These documents embody the additional steps, beyond defining individual species habitat needs, required to apply the kinds of information contained in this report in water quality and habitat restoration programs.

The two contaminants synthesis chapters: EFFECTS OF CONTAMINANTS ON SHELLFISH AND FINFISH and EFFECTS OF CON-

TAMINANTS ON BIRDS (Chapters 22 and 23), although they may seem to offer more questions than answers, are additional steps toward synthesis and understanding of complex habitat issues. A large amount of information on contaminant effects also is contained in the text and tables of several individual chapters (e.g., EASTERN OYSTER and BLUE CRAB). Although necessarily uneven (because of the uneven emphasis of available research), this material may help interested readers to form a more complete idea of the significance of contaminants for the Bay's resources.

Further synthesis needs can be identified. More complete syntheses of contaminants concerns for living resources should be developed, with reference to the large body of exposure and effects data that is becoming available for Chesapeake Bay species and habitats. This will be no small task, because of the enormous complexity of the field and the wide variety of data sources and sometimes questionable data quality. A synthesis of physical habitat requirements and problems would benefit greatly the growing efforts to restore and protect physical habitats (wetlands, vegetated shorelines, migration routes, salinity regimes, benthic substrates, etc.) by helping to establish priorities and to assure that these actions are not undertaken in isolation from each other.

Target Species

The selection of target species was done during the development of the first edition. The target species were selected to characterize all habitat types and trophic levels in Chesapeake Bay with a manageable subset of representative species. Initially, an extensive list of species was identified to represent all aquatic habitats, salinity and depth zones, and trophic levels. Selection of the target species from the larger list was based upon commercial, recreational, ecological, and aesthetic significance. The target species, through habitat and food chain associations, are intended to be surrogates for the larger ecosystem with its manifold valuable species. We note that the black-crowned night heron, one of the colonial wading birds, was not included among the target species in the first edition.

The target species are:

Plants

Ruppia maritima (widgeon grass)
Zostera marina (eelgrass)
Vallisneria americana (wild celery)
Potamogeton pectinatus (sago pondweed)
Potamogeton perfoliatus (redhead grass)

Invertebrates

Crassostrea virginica (eastern oyster)
Mya arenaria (soft shell clam)
Mercenaria mercenaria (hard clam)
Callinectes sapidus (blue crab)

Finfish

Brevoortia tyrannus (Atlantic menhaden)
Anchoa mitchilli (bay anchovy)
Alosa sapidissima (American shad)
Alosa mediocris (hickory shad)
Alosa pseudoharengus (alewife)
Alosa aestivalis (blueback herring)
Leiostomus xanthurus (spot)
Morone americana (white perch)
Morone saxatilis (striped bass)
Perca flavescens (yellow perch)

Waterfowl and Colonial Wading Birds

Aix sponsa (wood duck)
Anas rubripes (black duck)
Aythya valisineria (canvasback)
Aythya americana (redhead)
Ardea herodias (great blue heron)
Casmerodius albus (great egret)
Egretta thula (snowy egret)
Egretta caerulea (little blue heron)
Butorides striatus (green-backed heron)
Nycticorax nycticorax (black-crowned night heron)

Raptors

Pandion haliaetus (osprey)
Haliaeetus leucocephalus (bald eagle)

Organization

Each chapter summarizes published and unpublished literature pertinent to each target species or group of related species, organized into the following sections:

Abstract, Introduction, Background, Life History, Ecological Role, Habitat Requirements, Special Problems, Recommendations, and Conclusions.

Life History

The life history summaries in each chapter describe the species' morphology, development, growth, metamorphosis (e.g., from larva to juvenile in fish and invertebrates), recruitment (survival to an age of stable mortality rate), sexual maturity, mating, and mortality. In addition to describing the life stages of the species, the life histories recount their migrations, feeding habits and behavioral patterns. Life histories, habitat requirements, and ecological relationships all are overlapping components of the description of a species. Knowledge of life history is essential in identifying life stages that may be particularly vulnerable to pollution.

Ecological Considerations

Ecological considerations include the dynamic interplay of species with each other, whether the relationships are dependent (e.g., bay anchovy relying upon zooplankton),

independent (e.g., striped bass and great blue heron preying on common food sources), or indirect (e.g., waterfowl dispersing SAV seeds via defecation). Ecological considerations include the common benefits to be derived by non-target species if habitat conditions are satisfied for target species. Each chapter describes the ecological role of a species within the larger ecosystem, and how changes in the ecosystem influence a species' ability to function.

Habitat Requirements

The habitat requirements of individual species are numerous and complex; they include all abiotic and biotic environmental conditions necessary for a species to survive and reproduce. Abiotic conditions include factors such as water quality, substrate, circulation patterns, bathymetry, and weather; two dominant factors are salinity and depth. Biotic conditions are governed by variables such as vegetative cover, quality and quantity of prey species, predation, competition, parasites and diseases, population density, and primary production.

Habitat types in Chesapeake Bay are characteristic of a coastal plain estuary. They range from deep-water habitats in the mainstem Bay and lower tributaries to expansive saltwater marshes in the southeastern areas of the Bay. Tidal pools and flats are common as are shallow waters abutted by cliffs. Pine and hardwood forests follow shorelines and cover vast inland areas of the watershed. Underwater prairies of bay grasses provide hiding places for myriad life forms. Tidal fresh marshes are common in the upper tributaries. Definitive descriptions of estuarine and wetland habitats are available; readers are encouraged to refer to references devoted to habitat classification. The first edition of this report briefly described habitat zonation (upland shores, intertidal waters, shallow water, mid-water, and deep water) and salinity zones (tidal fresh, oligohaline, mesohaline, and polyhaline).

Authors were requested to provide existing information on the following specific habitat requirements:

WATER QUALITY

Dissolved Oxygen
Salinity
Turbidity
Temperature
Light
Nitrogen
Phosphorus
pH
Alkalinity and Hardness

STRUCTURAL HABITAT

Substrate
Vegetation
Water Depth
Water Flow
Shoreline Morphology

INTRODUCTION

Information on optimum as well as minimum or tolerable habitat conditions is presented, particularly for water quality. Optimum levels are important in setting habitat goals that will help restore a species to historic population levels. Defining minimum limits is important in deciding which species are particularly sensitive and need immediate attention.

Concluding Remarks

The authors and editors of this report have attempted to achieve a comprehensive and up-to-date compilation of information on the target species and their habitat requirements. Nevertheless, the report represents only a portion of available information on habitats in Chesapeake Bay, and highlights many unanswered questions about the status of populations, ecological relationships, and habitat requirements.

Readers are asked to pay particular attention to the many gaps in our knowledge of habitat requirements that have been identified both explicitly and implicitly by the chapter authors. Each chapter contains recommendations for research and monitoring to improve knowledge of the

species and their habitat needs. We hope that these recommendations will be used to establish research priorities. Research into such basic matters as life history, trophic function (what does a species eat?), and habitat needs (e.g., how much light or dissolved oxygen does it require for growth, survival, and reproduction?) should not be neglected. At the same time, research should address the quantification and prediction of benefits and risks to the ecosystem that are inherent in managing its components.

Finally, each chapter contains management recommendations, which should be viewed as complementary to the habitat information. It is clear that reliable management of living resources that are harvested requires simultaneous attention to harvest and habitat; attainment of habitat requirements alone cannot guarantee the establishment of specific population or harvest levels. For species that are not harvested, habitat management is the only tool available with which to manage the resource. We believe that this report is a significant step towards comprehensive scientific management of Chesapeake Bay living resources.

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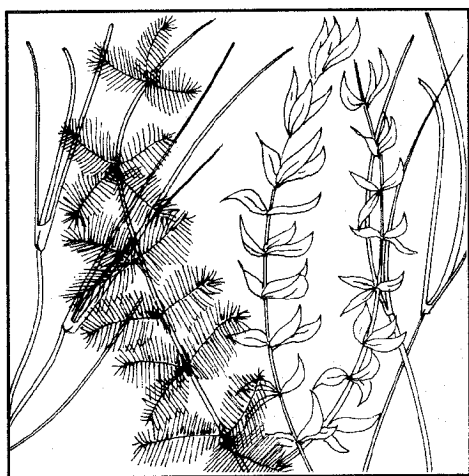
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SUBMERGED AQUATIC VEGETATION

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Five prominent species of submerged aquatic vegetation (SAV) representing four salinity regimes within Chesapeake Bay were selected for development of habitat requirements: wild celery, sago pondweed, redhead grass, widgeon grass, and eelgrass. Submerged aquatic vegetation provides habitat for fish and wildlife, food for waterfowl, absorbs nutrients, reduces suspended sediments, stabilizes substrates, and produces dissolved oxygen.

The Baywide decline of SAV has been attributed to reduced light availability from excessive water turbidity and biofouling of the plants caused by excessive loadings of nutrients and sediments from the surrounding Chesapeake watershed. The habitat requirements most important for SAV are those water quality parameters related to light attenuation: dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), total suspended solids (TSS), chlorophyll *a*, Secchi depth, and light attenuation (K_d). The threshold levels of these parameters necessary to maintain current SAV populations are presented. To return SAV to former historic levels of distribution and abundance, protection must be provided to remaining SAV populations, and excessive nutrient and sediment loadings must be reduced.

INTRODUCTION

Submerged aquatic vegetation (SAV) refers to underwater vascular plants. There are 15 species of SAV commonly found in Chesapeake Bay and its tidal tributaries. Species distributions are mainly determined by their salinity tolerance. The five species in this report are species that represent the range of salinity regimes that occur within the Bay. Wild celery and sago pondweed occur in tidal fresh (0-0.5 ppt), oligohaline (0.5-5 ppt), and mesohaline waters (5-18 ppt). Redhead grass inhabits oligohaline and mesohaline salinities. Widgeon grass and eelgrass are found in both the mesohaline and polyhaline zones (18-30 ppt).

Submerged aquatic vegetation performs a number of valuable ecological roles within the Bay. The plants are a major food source for Bay waterfowl.^{49,53} The beds provide a habitat and shelter for a variety of fish, shellfish, and many small invertebrates.^{1,47,57,58,66} SAV contributes to chemical processes such as nutrient absorption and

oxygenation of the water column.¹¹ Dense SAV beds also aid in baffling wave energy and slowing water currents thus reducing resuspension of bottom sediments and shoreline erosion as well as promoting settlement of suspended sediments.⁸⁷

Submerged aquatic vegetation has been a vital component of the Bay ecosystem since pre-colonial times. Records of SAV seeds collected from sediment cores taken around the Bay show that SAV was present prior to European settlement.¹² Historically, SAV has generally been abundant throughout the Chesapeake Bay.⁵⁹ Today, only about 24,000 hectares remain.⁶⁰ The drastic decline of SAV, first noted in the 1970's, sparked the interest of Bay scientists and managers to determine the cause for this significant loss and seek methods to restore this dwindling resource.^{13,29,43,44,84,89}

Early observations suggested that the SAV decline may be attributed to natural population cycles or weather events such as droughts and hurricanes. Excessive grazing and

foraging by various animals, industrial pollutants and agricultural herbicides were also explored as possible explanations for the decline. However, after many years of research, it is now a consensus of Bay scientists that the recent loss of SAV in Chesapeake Bay is due to decreased light penetration throughout the water column and biofouling of the plant surfaces caused by excessive loadings of nutrients and sediments from the surrounding Chesapeake Bay watershed.^{43,44,76,78,84}

Nutrients are supplied to the Bay's waters predominantly by fertilizers associated with agricultural runoff and by municipal wastewater treatment discharges. Sediment inputs to the Bay are attributed to agricultural and urban runoff and by shoreline erosion. The excessive nutrient and sediment loadings cause increases in turbidity, therefore, limiting light necessary for the plants to grow and reproduce. Nutrient enriched waters stimulate dense algae blooms in the water column and epiphytic growth on the plants which reduce light transmittance to SAV. This results in a reduction of photosynthesis with a subsequent loss of carbohydrate reserves necessary for plant production. Reduced light penetration is exacerbated by sediments suspended both in the water column and covering the plant stem and leaf surfaces.^{43,76,78,84}

Habitat requirements most applicable to SAV are those water quality parameters that directly measure or contribute to light attenuation. The key parameters identified are: dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), total suspended solids (TSS), chlorophyll *a*, Secchi depth and light attenuation (*K_d*).

BACKGROUND

The five species covered in this report are commonly found in the Chesapeake Bay: wild celery (*Vallisneria spiralis*), sago pondweed (*Potamogeton pectinatus*), redhead grass (*P. perfoliatus*), widgeon grass (*Ruppia maritima*) and eelgrass (*Zostera marina*). A brief description of each species along with a discussion of their range and distribution in Chesapeake Bay and their individual population status and trends follows.

Wild Celery

Also called tapegrass or freshwater eelgrass, wild celery gets its common name because of its resemblance to a stalk of celery with whitened, lower leaf ends rising from the plant base. The leaves are long, flat, and ribbon-like with rounded tips. Individual plants grow from nodes along an underground rhizome. Wild celery is primarily a freshwater species capable of tolerating oligohaline and mesohaline water. It is generally found growing in coarse silt to slightly sandy soil. Wild celery can tolerate wave action and currents fairly well compared to more delicately leaved and rooted SAV.^{33,76,78}

Wild celery occurs along the Atlantic Coastal Plain west through Minnesota. In the Chesapeake Bay, seed records show wild celery was abundant from pre-colonial times to the 1930's in the upper Bay and tributaries such as Furnace Bay, Back, Middle, Severn, Patuxent, and Chester Rivers. Since the 1970's, a dramatic decline in wild celery in these areas has occurred. Today, wild celery is most abundant in the Susquehanna River and Flats region and in the tidal fresh, oligohaline, and mesohaline zones of the Potomac River. It is also reported, although less frequently, from the Elk, Sassafras, Middle and Gunpowder rivers (Map Appendix).^{8,12,13,60,76,78}

Sago pondweed

Sago pondweed has long, narrow, thread-like leaves that taper to a point. The abundantly branched and slender stems create bushy clusters of leaves that fan out at the water's surface. Sago pondweed has slender rhizomes, which are long and straight, that provide strong anchorage to the substrate making it able to withstand water currents and wave action fairly well. In the Chesapeake Bay region, sago pondweed is found growing in tidal fresh to mesohaline waters (up to 9 ppt), and in sediments that are generally of a silt-mud composition.^{33,76,78}

Sago pondweed is widely distributed throughout the United States and Canada. In the United States it is most abundant in the northwestern states and the Chesapeake Bay. An SAV survey begun in 1971 in the Maryland portion of the Bay showed sago pondweed distributed from the Chester River south into Tangier Sound on the Eastern Shore and in the Severn and Patapsco Rivers on the Western Shore. By 1976 only Eastern Bay and Chester River reported any sago pondweed. Today, it is reported in the tidal Potomac River as far down as the Port Tobacco River. It is also reported in the Middle, Chester, and Choptank Rivers and the Susquehanna Flats area. Although reports of sago pondweed have increased in recent years, population densities are far below earlier levels (Map Appendix).^{8,12,13,60,76,78}

Redhead grass

This species is easily distinguished from other SAV by its flat, oval-shaped leaves, the base of which clasps the plant stems. The leaves are usually arranged alternately or slightly opposite and the leaf margins are slightly crisp. The stems of redhead grass are straight and slender, becoming more branched toward the upper portion of the plant. Due to the extensive root and rhizomes system, redhead grass is securely anchored in the substrate. Like sago pondweed, redhead grass is typically found in tidal fresh to mesohaline waters. Firm, muddy soils and quiet waters with slow-moving currents seem to be preferred.^{33,76,78}

Seed records show redhead grass to be common in pre-colonial times and sporadic during the 1700's to 1930.

Redhead grass was extremely prevalent from the 1930's to 1970. From 1971 to 1976 redhead grass was reported in Eastern Bay, the Choptank, Severn, and Chester Rivers. The Patapsco and Magothy Rivers reported redhead grass up to 1974. Today, redhead grass occurs predominately in Susquehanna Flats, Chester River, and the mid-section of the Potomac River near Mathias Point, Port Tobacco River and Nanjemoy Creek (Map Appendix).^{8,12,13,60,76,78}

Widgeon grass

Widgeon grass has linear, thread-like leaves arranged alternately along the slender, branching stems. There is an extensive root system made up of many branched, creeping rhizomes. This species tolerates a wide range of salinities and occurs in a wide variety of habitats. Although it occasionally is found growing on soft, muddy sediments, it is more common on sandy substrates. This species is also known as ditch-grass because it is commonly found growing in shallow tidal marsh ditches. The slender stems of widgeon grass are easily damaged by high wave action.^{33,76,78}

Widgeon grass is reported from the Atlantic, Pacific, and Gulf Coasts as well as the Great Salt Lake region. Seed records show widgeon grass was present in the Chesapeake Bay during pre-colonial times and distributed in much the same patterns as today. Widgeon grass started to decline in the 1960's and 1970's. A slight downward trend from 1971 to 1980 was followed by sharp reductions in the early 1980's. Surveys in 1985 and 1986 showed an increase in mid-Bay waters, especially the Chester and Choptank Rivers. By 1989, widgeon grass had increased significantly in the lower Rappahannock and Piankatank Rivers on the Eastern Shore, and in Eastern Bay, the Choptank and the Barren Island-Honga Rivers of the mid-Bay (Map Appendix). Today widgeon grass is the most abundant and widely distributed SAV species in Chesapeake Bay.^{8,12,60,76,78}

Eelgrass

Eelgrass has linear, ribbon-like leaves with rounded tips, deriving its Latin name from the Greek word *zoster* meaning belt or strap. The leaves occur singularly and alternately along the joints of the stem. The length and width of eelgrass leaves can vary depending on the type of habitat. A short, narrow-leaf form generally occurs in areas of shallow, high-energy waters while a long, wide-leaf form is more common in deeper, less exposed waters. Eelgrass has thick, creeping rhizomes with numerous roots.^{33,76,78}

Eelgrass, unlike other Chesapeake Bay SAV, is a true "seagrass" and is found in salinities of 10 to 35 ppt. Both eelgrass and widgeon grass can occur in many of the same areas of the lower Bay, but eelgrass does not appear to grow as well as widgeon grass in shallow water. Eelgrass grows primarily on sandy substrates in the Chesapeake Bay.^{33,76,78}

Eelgrass is found on both the Atlantic and Pacific coasts of North America and along northern European coastlines. In Chesapeake Bay, it is found in the mesohaline and polyhaline areas of the lower Bay. Through seed records, it has been shown that eelgrass has been present in the Bay since pre-colonial times and retained a fairly stable abundance from 1720 to 1880. Historic distributions were located in the lower sections of the major tributaries of the lower Bay including the Potomac, Patuxent, Rappahannock, James, Piankatank, and York Rivers of the western shore and from Eastern Bay south on the Eastern Shore. During the 1930's eelgrass underwent a severe decline on both sides of the north Atlantic, probably due to disease. Although eelgrass recovered to some extent during the 1950's and 1960's, a significant decline occurred during the 1970's throughout Chesapeake Bay. Today, eelgrass is located mainly along the Eastern Shore from Smith Island south to Cape Charles. The largest concentrations in this area are between Smith, Tangier, and Great Fox Islands, and at the mouths of the major creeks from Cherronessex south. The largest distributions of eelgrass along the western shore include the Back, Poquoson, and York Rivers and Mobjack and Fleets Bays (Map Appendix).^{8,12,60,76,78}

The potential habitat distribution for all species of SAV in Chesapeake Bay has been developed⁸ (Map Appendix). The distribution is based upon the composite mapping of all available SAV distribution data, both historic and present, and the 2 m depth contour of the Chesapeake Bay. The 2 m depth contour was included because it is the predicted SAV distribution for most species when their habitat requirements are achieved Baywide.

LIFE HISTORY

All five species of SAV in this report are capable of sexual and asexual reproduction, the modes of which vary from species to species.

Wild celery

Asexual reproduction is by elongation of the underground rhizomes from which new plants emerge at the ends. Vegetative tuber production commonly takes place. The thick overwintering tubers grow on the ends of underground runners that branch off the rhizomes.^{33,76,78}

Sexual reproduction regularly occurs in wild celery usually in late July through September. Wild celery is dioecious. The numerous staminate flowers are crowded together and enclosed in an ovoid spathe borne on a short peduncle at the base of the plants. The pistillate flowers occur singularly in a tubular spathe on the end of an exceedingly long peduncle that grows to the water surface from the plant base. The pistillate flowers have three sepals and three white petals. The spathe containing the staminate flowers eventually breaks free and floats to the

water surface where the flowers are released and float into contact with the female flowers. Once fertilization is complete, the peduncle of the pistillate flower coils up and draws the developing fruit underwater. A long, cylindrical pod is produced that contains many small, dark seeds.^{33,76,78}

Sago pondweed

Sexual reproduction occurs during early summer by formation of a spike of perfect flowers that appear like beads on the slender stalk. Pollen is released from the flowers and floats on the water surface resulting in fertilization. The developing seeds remain on the rachis of the spike until autumn when they are dispersed in the water. Germination rates are generally reported as low, making vegetative reproduction more significant.^{33,76,78}

Asexual reproduction is by production of starchy tubers at the ends of the underground rhizomes and runners and by smaller tubers that develop in the leaf axils at the end of the leaf shoots. These latter structures occur singularly or in pairs and are later released and sink to the substrate. After overwintering, both kinds of tubers form new plants in the spring.^{33,76,78}

Redhead grass

Sexual reproduction regularly occurs in redhead grass during early to mid-summer. Spikes of tiny flowers emerge from leaf axils on the ends of the plant stems and extend above the water surface. Pollen is released into the air and carried by the wind for fertilization. As the fruits mature, they sink back below the surface and the seeds are later released to the sediments. Asexual reproduction occurs by formation of resting buds at the end of the many rhizomes. These overwinter and become new plants in spring.^{33,76,78}

Widgeon grass

Asexual reproduction is through extension of the root-rhizome system from which new stems emerge. Sexual reproduction commonly occurs with flowering usually taking place in late summer. There are two, tiny perfect flowers enclosed together in the sheathing base of the leaves. As the flowers mature, they are extended upward towards the water surface by elongation of a peduncle or flower stalk. The pollen grains are later released from the stamens and float on the surface until making contact with one of the extended pistils. Each fertilized flower produces four oval-shaped fruits that are black with pointed tips. The individual fruits are extended on separate slender stalks with up to eight in a cluster.^{33,76,78}

Eelgrass

Asexual reproduction is by growth of the creeping, grass-like rhizomes from which new stems are produced. Flower and seed production take place during spring in Chesapeake Bay. Eelgrass is monoecious. The male and

female flowers are arranged alternately, in two rows, along a spadix or spike, which is enclosed in a long spathe or the sheath-like base of the leaf. Fertilization occurs when thread-like pollen grains drift into contact with the female flowers. The staminate flowers produce pollen before the pistillate flowers on the same plant are fully developed. This prevents self-fertilization from taking place. The plant shoots containing the seeds eventually break off and float to the surface where the seeds are dispersed as the shoots are carried along by the water currents. Seeds can also be dispersed in the surrounding sediments before the shoots are detached. Seed germination takes place during autumn when water temperatures start to decline. The changing photoperiod or daylength may also induce germination.^{33,76,78}

In Chesapeake Bay, the highest productivity for eelgrass occurs during the spring and fall. In the cold winter months, eelgrass continues to grow, although much more slowly. But, during the summer when water temperatures are high, researchers have suggested that eelgrass becomes heat stressed and its growth markedly declines. This makes eelgrass unique among other Bay grasses which have their highest growth periods during the summer.^{33,76,78}

ECOLOGICAL ROLE

The ecological role of SAV in the Chesapeake Bay ecosystem is complex. The plants serve as both a food source and a habitat and nursery area for many invertebrates and vertebrates. SAV also contributes to primary production, nutrient absorption, and dissolved oxygen production.^{11,76,78}

The value of SAV as food to waterfowl cannot be overstated. Several different species of duck, geese, and swans depend on SAV as a major portion of their diet. Most parts of the plants are palatable. Besides the nutritious seeds and tubers, the root stalks are often consumed by these birds. The names of three SAV species indicate their importance to waterfowl. For example, one of the major foods of the redhead is redhead grass. Widgeon grass gets its common name from the widgeon. The scientific name of the canvasback, *Aythya valisineria*, demonstrates its connection to wild celery of a similar Latin name, *Vallisneria americana*. Sago pondweed and eelgrass are also highly nutritious for waterfowl. Population declines of Chesapeake Bay waterfowl have been attributed to the loss of SAV. Canvasbacks and redheads are at record low numbers while many other species show similar downwards trends. Brant geese underwent a precipitous decline as its principal food source eelgrass disappeared in the 1930's. Turning to less nutritious food such as algae enabled this species to survive.^{11,49,53,76}

SAV's role as a habitat and nursery area for many species of fish and invertebrates is well documented. Vegetated areas generally yield significantly greater fish density, biomass, and species richness than non-vegetated areas. Beds of aquatic plants with their numerous leaves and stems provide cover for many small prey species such as minnows, killifish, and juvenile spot. Hard crabs and the vulnerable molting softshells find cover from predators among the plant beds. Eelgrass beds in the lower Bay are important habitat for juvenile blue crabs, while the leaves of eelgrass serve as a setting substrate for the Bay scallop.^{1, 11, 57, 58, 66}

There is a diverse assemblage of food sources within plant beds for many Bay species. For example, algae, eggs, barnacles, and bryozoans can be found attached to the surface of plant leaves and stems. Other organisms live among the plant roots in the sediment. These are grazed upon by such animals as snails, worms, and other invertebrates which in turn provide food for larger fish and invertebrates such as crabs.⁴⁷

SAV also helps to stabilize sediments and slow water currents. This allows suspended sediments to settle out and reduces resuspension of bottom sediments thus lowering turbidity. Reduced turbidity is beneficial to an assortment of benthic filter feeders including oysters and clams.^{11, 87}

WATER QUALITY HABITAT REQUIREMENTS

The major habitat parameter that controls SAV distribution is light attenuation.^{8, 23, 43} Light attenuation (reduction in light intensity) in the water column is due to light absorption by water molecules and suspended particles. Light attenuation can be measured in two ways: (1) with a light meter to calculate light attenuation coefficients (K_d) based on an exponential decay function; and (2) by Secchi depth measurements. Chlorophyll *a* and other suspended solids are responsible for the majority of the total light attenuation in the water column. Chlorophyll *a* is a pigment found in all photosynthetic phytoplankton. Measurements of chlorophyll *a* concentrations are used as indicators of phytoplankton biomass and, therefore, indirectly provide a measure of nutrient loading. Total suspended solids (TSS) is a measure of suspended inorganic solids, plus microorganisms and organic detritus.

Nutrients, such as nitrogen and phosphorus, are also important habitat parameters because they indirectly contribute to light attenuation by stimulating growth of phytoplankton within the water column and algal epiphytes on SAV leaves and stems. These parameters are measured as DIN and DIP. Additional habitat parameters such as temperature and pH generally do not limit SAV whereas salinity requirements are species specific.

Habitat requirements for SAV in Chesapeake Bay are largely drawn from *Chesapeake Bay Submerged Aquatic Vegetation Habitat and Restoration Goals: A Technical Synthesis*.⁸ That document was in the final stages of preparation at the writing of this chapter. For further detail on the data presented therein, the reader is urged to obtain the document after its publication. Data on K_d , Secchi depth, TSS, chlorophyll *a*, DIN, and DIP were compiled from numerous laboratory, field, and mesocosm studies from four study regions of Chesapeake Bay as well as from reviews from historic and recent literature. The four areas of study include all salinity regimes of the Bay: upper Chesapeake Bay and the upper tidal Potomac River, which include both tidal fresh and oligohaline regions; the Choptank River for mesohaline SAV species; and the York River for polyhaline SAV species. Habitat requirements for these key parameters, as established through analysis and interpretation of data from the four case study areas, are discussed below and summarized in Table 1.

Dissolved Inorganic Nitrogen

Tidal Fresh - Oligohaline (wild celery, sago pondweed)

In tidal fresh and oligohaline habitats, no DIN habitat requirement has been established as a threshold level because DIN was not conclusively associated with SAV distribution and abundance in the upper Chesapeake Bay and Potomac River study regions. In these low salinity habitats, DIP is believed to be the limiting nutrient for phytoplankton and epiphytic growth.

Upper Chesapeake Bay: no clear relationships between SAV growth and DIN concentrations were found for the upper Chesapeake Bay region. The presence or absence of naturally occurring SAV populations and success of transplanted SAV plots could not be correlated with DIN concentrations.

Potomac River: dissolved inorganic nitrogen was not measured directly in the Potomac River, but was calculated from data for ammonia (NH_4) and nitrate (NO_3) plus nitrite (NO_2) available from several data sets collected by a number of state and Federal agencies spanning the 10-year period 1980-1989. Concentrations ranged from about 2 mgL^{-1} in the upper tidal river near Washington, D.C., to about 0.5 mgL^{-1} in the oligohaline zone near Maryland Point in 1980. Concentrations at Maryland Point were $> 1.5 \text{ mgL}^{-1}$ by 1989.

Ammonia may influence SAV survival more than DIN because of its influence on algal growth.⁶⁹ When ammonia concentrations were $> 0.6 \text{ mgL}^{-1}$ in 1980, SAV was not present in the upper tidal river. Revegetation occurred, however, in the upper tidal river when median ammonia concentrations decreased to $\leq 0.4 \text{ mgL}^{-1}$.

Established beds of SAV in the oligohaline region were able to survive under median ammonia concentrations of $0.4\text{--}0.7\text{ mgL}^{-1}$. For both the fresh and oligohaline portions of the river, median nitrate plus nitrite concentrations of $\leq 1.7\text{--}2\text{ mgL}^{-1}$ were compatible with SAV propagation and survival from 1983 to 1989.

Mesohaline (sago pondweed, redhead grass, widgeon grass)

For mesohaline waters, the habitat requirement for DIN is $< 0.15\text{ mgL}^{-1}$, as determined through analysis of data from the Choptank River study region (Table 1). Seasonal concentrations above this level were associated with the absence of SAV. This threshold value was based upon comparisons between seasonal median DIN concentrations and the distribution and abundance of SAV in the Choptank River. During 1986-1989 monthly DIN concentrations were determined over the SAV growing season of April through September in areas of the river containing dense SAV populations, and areas where SAV growth was sparse or absent. In the upper reaches of the Choptank River where no SAV occurred, DIN concentrations ranged from $0.15\text{--}0.26\text{ mgL}^{-1}$ during 1986-1988, a period of low summer rainfall. In 1989, a wet year, median DIN concentrations rose to 1.12 mgL^{-1} . In the lower portions of the river where SAV occurred, median DIN for 1986-1988 ranged from $0.06\text{--}0.07\text{ mgL}^{-1}$ and were 0.23 mgL^{-1} in 1989. The DIN threshold concentration of 0.15 mgL^{-1} was selected based upon the general absence of SAV populations in the Choptank River where seasonal median DIN concentrations exceeded 0.15 mgL^{-1} .

Polyhaline (widgeon grass, eelgrass)

The DIN habitat requirement for SAV in polyhaline waters is $< 0.15\text{ mgL}^{-1}$ (Table 1). This value was determined from biweekly water quality samples taken during 1984-1989 from several sites in the York River. Sample sites were located along a gradient from the river mouth where healthy SAV beds existed to the upriver limits of SAV growth. The DIN threshold value of 0.15 mgL^{-1} is the combined spring/fall growing season median at vegetated sites over the 6-year sampling period. Median DIN concentrations increased with distance upriver whereas SAV abundance decreased. Higher DIN levels (0.35 mgL^{-1}) were observed during winter at some vegetated sites. However, little difference in SAV growth occurred, most likely due to lower water temperatures and light levels during this period. Phytoplankton and epiphytic algae biomass also were lower during the winter months accounting for the higher DIN levels (i.e., algal demand for nutrients was reduced).

Dissolved Inorganic Phosphorus

Tidal Fresh - Oligohaline (wild celery, sago pondweed)

The habitat requirement for DIP of $< 0.02\text{ mgL}^{-1}$ for tidal fresh and oligohaline habitats is based on the findings

from analysis of data from the upper Chesapeake Bay study region. In the Potomac River study region, DIP concentrations associated with SAV revegetation and expansion were higher, $\leq 0.04\text{ mgL}^{-1}$ in the tidal fresh and $\leq 0.04\text{--}0.07\text{ mgL}^{-1}$ in the oligohaline habitats.

Upper Chesapeake Bay: concentrations above 0.02 mgL^{-1} of DIP are associated with reduced SAV abundance in the upper Chesapeake Bay (Table 1). This value of DIP is the seasonal median of monthly samples taken from April through October during 1989 from 32 sites stationed throughout the upper Bay. During 1989 a decline in SAV occurred in this region compared to 1987-1988 distributions. Sampling sites with median DIP concentrations $> 0.02\text{ mgL}^{-1}$ were associated with marginal SAV growth while sites with median DIP $< 0.02\text{ mgL}^{-1}$ still supported abundant SAV.

Similar trends in phosphorus loadings occurred in 1987-1988; however, orthophosphate (unfiltered) rather than DIP was measured. Seasonal medians of orthophosphate $< 0.02\text{ mgL}^{-1}$ were associated with sites supporting abundant SAV compared to unvegetated sites.

Potomac River: present median concentrations of DIP in the Potomac River, $\leq 0.04\text{ mgL}^{-1}$ in the tidal fresh and $\leq 0.04\text{--}0.07\text{ mgL}^{-1}$ in the oligohaline habitat, support SAV revegetation and expansion. These levels are much reduced from historic levels of the 1960's. For example, in 1969, DIP concentrations as high as $0.15\text{--}0.36\text{ mgL}^{-1}$ were recorded. However, DIP concentrations generally have remained $\leq 0.04\text{ mgL}^{-1}$ in the tidal fresh and between $0.04\text{--}0.07\text{ mgL}^{-1}$ in the oligohaline areas since about 1980. SAV returned to the Potomac River in 1983 after being reported absent from the river during a 1978 survey.²⁹ Because DIP concentrations have remained relatively constant when SAV was absent from the river and since SAV had returned, no strong conclusions can be made regarding the threshold concentrations of DIP for SAV in the Potomac River.

Mesohaline (sago pondweed, redhead grass, widgeon grass)

The seasonal median concentration of DIP associated with SAV growth and survival in mesohaline habitats is $< 0.01\text{ mgL}^{-1}$ (Table 1). During 1986-1988, years of successful SAV recolonization in the Choptank River, seasonal median DIP ranged from 0.005 to 0.009 mgL^{-1} in the lower Choptank, suggesting 0.01 mgL^{-1} as the threshold concentration for SAV growth. In contrast, at historic upriver SAV locations where SAV was absent during 1986-1988, seasonal median DIP concentrations ranged from 0.03 to 0.04 mgL^{-1} .

Polyhaline (widgeon grass, eelgrass)

The threshold level of DIP associated with SAV growth in polyhaline habitats is $< 0.02\text{ mgL}^{-1}$ (Table 1). Based on

1984-1989 biweekly sampling, increasing levels of DIP occurred with distance upriver during most seasons, corresponding with a decreasing SAV distribution and abundance gradient in the York River. The highest seasonal medians of DIP during this period at vegetated sites were $< 0.02 \text{ mgL}^{-1}$. Dissolved inorganic phosphorus levels exceeded this level at upriver non-vegetated sites.

Light Attenuation and Secchi Depth

The threshold levels of light attenuation (K_d) reported from the four salinity regions of the Chesapeake Bay ranged from < 1.5 to $< 2.7 \text{ m}^{-1}$. Secchi depths for the four regions ranged from ≥ 0.5 to $> 0.8 \text{ m}$ (Table 1).

Tidal Fresh - Oligohaline (wild celery, sago pondweed)

Upper Chesapeake Bay: in the upper Bay, abundant SAV beds existed during 1989 at sampling stations where $K_d < 2.0 \text{ m}^{-1}$, whereas vegetated stations with $K_d > 2.0 \text{ m}^{-1}$ had lost over one-half of their 1988 coverage. Secchi depth measurements taken during 1987-1988 showed that a seasonal median Secchi depth $> 1.0 \text{ m}$ was associated with the presence of SAV at most sites. SAV beds at protected sites (i.e., areas of reduced current and wave energy) were able to tolerate slightly reduced light penetration with seasonal median Secchi depth $> 0.8 \text{ m}$. These values, 1.0 m and 0.8 m , correspond to the K_d values of 1.45 m^{-1} and 1.8 m^{-1} respectively. The conversion factor, $K_d = 1.45/\text{Secchi depth}$, was developed for the Chesapeake Bay by simultaneous measurements of both Secchi depth and K_d .

Potomac River: in the Potomac River an analysis of data collected over the period 1980-1989 showed that SAV survival in the tidal fresh zone was unlikely at a seasonal median Secchi depth $\leq 0.5 \text{ m}$ and seasonal median Secchi depths $\geq 0.7 \text{ m}$ were necessary for revegetation and expansion. Between these limits, survival may depend on amount of available sunshine, epiphyte loading, etc. In the oligohaline portion of the river some survival of established SAV populations occurred at Secchi depth as low as 0.5 m . Results of 1985-1986 light attenuation studies showed that seasonal median K_d levels were significantly greater in the lower tidal fresh river than in the upper tidal fresh portion. These high levels were associated with significantly less SAV in the lower freshwater portion than in the upper tidal reaches. Revegetation and increasing abundance of SAV was found when seasonal median K_d was $\leq 2.2 \text{ m}^{-1}$ (Table 1). When seasonal median K_d was $\geq 2.4 \text{ m}^{-1}$ revegetation did not occur. Previously established SAV beds in the oligohaline portion of the river survived when seasonal median K_d values were as high as 2.7 m^{-1} .

Mesohaline (sago pondweed, redhead grass, widgeon grass)

In mesohaline habitats, $K_d < 1.5 \text{ m}^{-1}$ is associated with SAV growth and survival based on findings from analysis of data from the Choptank River study region (Table 1). In the uppermost sections of the Choptank River (40 km above the mouth) where SAV is absent, K_d of 2.0 m^{-1} and above is common. During the dry years 1986-1988, the mid-river section (20 km to 40 km) had marginal SAV growth while in the lowest portion of the river (below 20 km) SAV revegetation was extensive. Seasonal median K_d values during this period were $< 2.0 \text{ m}^{-1}$ and $< 1.5 \text{ m}^{-1}$, respectively. Furthermore, in the wet year of 1989 when SAV growth declined throughout the river, K_d values exceeded 1.5 m^{-1} up to 18 km above the river mouth which included areas that had previously supported abundant SAV. Therefore, K_d values $< 1.5 \text{ m}^{-1}$ correlated with abundant SAV growth and $K_d < 2.0 \text{ m}^{-1}$ correlated with marginal SAV growth (Table 1).

Polyhaline (widgeon grass, eelgrass)

In polyhaline habitats, the SAV habitat requirement for K_d is $< 1.5 \text{ m}^{-1}$. Results reported for the polyhaline, lower Chesapeake Bay are similar to the mid-Bay region. During 1984-1989, K_d levels in the York River increased with distance upriver along with a concomitant decrease in SAV. The seasonal median K_d at vegetated sites was $< 1.5 \text{ m}^{-1}$ (Table 1).

Chlorophyll *a*

The habitat requirement for chlorophyll *a* associated with SAV growth and survival for most areas of the Chesapeake Bay is $< 15 \text{ } \mu\text{gL}^{-1}$ (Table 1).

Tidal Fresh - Oligohaline (wild celery, sago pondweed)

Upper Chesapeake Bay: in the upper Chesapeake Bay during 1987-1989, SAV beds did not survive at sites in the Sassafras River when chlorophyll *a* exceeded $15 \text{ } \mu\text{gL}^{-1}$ except in shallow protected areas. At other sites in the Elk River and the Susquehanna Flats, chlorophyll *a* levels were generally below $15 \text{ } \mu\text{gL}^{-1}$.

Potomac River: in the tidal fresh to oligohaline Potomac River, seasonal median chlorophyll *a* values of $\leq 15 \text{ } \mu\text{gL}^{-1}$ were associated with revegetation and continued propagation of SAV. A downward trend in chlorophyll *a* occurred over the period 1980-1989 in these portions of the river along with an increase in SAV at all sampling stations. High chlorophyll *a* values ($> 30 \text{ } \mu\text{gL}^{-1}$) of short duration were noted but did not seem to be detrimental to established SAV beds.

Mesohaline (sago pondweed, redhead grass, widgeon grass)

Chlorophyll *a* reported from the Choptank River were similar to levels measured in the Potomac River. In the

lower portions of the river (0-20 km) where healthy SAV beds have persisted, the seasonal medians for chlorophyll *a* measured in 1988 and 1989 were $10 \mu\text{gL}^{-1}$. The middle reach of the river (20-40 km), a region of marginal SAV growth, had seasonal median concentrations of chlorophyll *a* of $6 \mu\text{gL}^{-1}$ in 1988 and $11 \mu\text{gL}^{-1}$ in 1989. In the uppermost river (above 40 km) where SAV is absent, seasonal median concentrations ranged from $17\text{-}20 \mu\text{gL}^{-1}$. Based on these data $15 \mu\text{gL}^{-1}$ is the uppermost limit whereas lower chlorophyll *a* concentrations of $< 10 \mu\text{gL}^{-1}$ may be necessary to sustain existing SAV populations in this mesohaline region (Table 1).

Polyhaline (widgeon grass, eelgrass)

A critical chlorophyll *a* habitat requirement of $< 15 \mu\text{gL}^{-1}$ was determined for the polyhaline region of the Bay. Seasonal median levels of chlorophyll *a* at vegetated sites were $< 15 \mu\text{gL}^{-1}$ during 1987-1989.

Total Suspended Solids

For most regions of the Chesapeake Bay, the TSS habitat requirement for SAV is $< 15 \text{ mgL}^{-1}$ (Table 1).

Tidal Fresh - Oligohaline (wild celery, sago pondweed)

Upper Chesapeake Bay: the seasonal median TSS concentration at which SAV survived in the upper Chesapeake Bay during the 1989 growing season was $< 15 \text{ mgL}^{-1}$ (Table 1). At sampling sites where median TSS concentrations were above 20 mgL^{-1} , SAV were not found during the same period. Levels below 10 mgL^{-1} were associated with a higher abundance of SAV.

Potomac River: seasonal median TSS concentrations of $\leq 15\text{-}16 \text{ mgL}^{-1}$ are required for SAV growth in the tidal fresh portion of the Potomac River (Table 1). Median concentrations of TSS over the growing season of April to October were measured during 1980-1989. During 1980 only the oligohaline portion of the river contained SAV. Seasonal median TSS concentrations in this reach of the river were $\leq 15\text{-}20 \text{ mgL}^{-1}$. In both the upper and lower tidal river, where no SAV was present during this period, seasonal median TSS concentrations ranged from $> 20\text{-}30 \text{ mgL}^{-1}$. During 1983-1989, a downward trend in TSS concentrations corresponded with the re-establishment of SAV in the tidal fresh portions of the river and the continued propagation of previously established SAV in the lower oligohaline reaches of the river. By 1986, and again in 1989 the entire length of the tidal fresh and oligohaline river portions contained SAV, whereas the seasonal median TSS concentrations ranged near 15 mgL^{-1} throughout these areas.

Mesohaline (sago pondweed, redhead grass, widgeon grass)

For mesohaline habitats the habitat requirement for TSS of $< 15 \text{ mgL}^{-1}$ is based on findings from the Choptank River

study region. In the Choptank River, areas of SAV growth and recolonization had seasonal median concentrations of TSS below 15 mgL^{-1} during most of the growing season (Table 1). In contrast, concentrations $> 20 \text{ mgL}^{-1}$ routinely occurred upriver where no SAV was present.

Polyhaline (widgeon grass, eelgrass)

The TSS habitat requirement for polyhaline habitats is $< 15 \text{ mgL}^{-1}$. The seasonal median of TSS measured at lower York River sites where SAV remains is $< 15 \text{ mgL}^{-1}$. TSS concentrations measured at upriver sampling sites where SAV is no longer present significantly exceeded this amount. Therefore, the median seasonal concentration of $< 15 \text{ mgL}^{-1}$ TSS is the habitat requirement for SAV in polyhaline waters (Table 1).

Temperature

The principal growth period for most Chesapeake Bay SAV species is from April to October. Optimum water temperatures for photosynthesis and growth generally range around 30°C and occur during the summer months. However, eelgrass grows best during spring and autumn when water temperatures are lower.^{8,76,78}

Wild celery

The most active growth for wild celery in the Chesapeake Bay is during the months of June, July, and August, although turion formation occurs in September.

In the upper Chesapeake Bay and in the Potomac River, wild celery germinates from overwintering tubers when water temperature is about 15°C . Growth of wild celery becomes more rapid with increasing temperature and the plants tolerate maximum water temperatures of $30\text{-}35^\circ\text{C}$.⁸

Comparable temperature ranges also are reported in the literature. Under laboratory conditions wild celery grew best within the temperature range of $33\text{-}36^\circ\text{C}$, whereas temperatures below 19°C caused arrested growth, and temperatures above 50°C caused plants to become limp and disintegrated.⁹¹ Similar ranges have been reported by others.^{6,7,78,80} In the Detroit River wild celery grew at a water temperature range of $19\text{-}31.5^\circ\text{C}$, while in Lake Erie, wild celery grew at $22.7\text{-}26.3^\circ\text{C}$.^{32,45,51}

Sago pondweed

Sago pondweed survives in a highly variable range of temperature, which partially explains its cosmopolitan distribution. Temperatures as low as 5°C have been reported as the lower threshold of sago pondweed growth.^{31,40} Under laboratory conditions the tolerance range for sago pondweed was $10\text{-}37^\circ\text{C}$, with highest growth rates occurring between 17 and 23°C .^{40,72,78}

Redhead grass

Optimum temperatures for photosynthesis and growth of redhead grass generally range about 30°C .⁷⁸ Respiration

and oxygen consumption of redhead grass has been shown to increase as temperatures increased from 25 to 40°C with death occurring at 45°C.^{2,76,78}

Widgeon grass

In Chesapeake Bay the seasonal temperature range for widgeon grass is 0-30°C. In the Choptank River, seasonal temperatures generally range from 2°C during the winter months to 30°C in the summer while in the York River, temperatures range from 0-30°C where widgeon grass is distributed.⁸

In other studies, widgeon grass growth is associated with a temperature range of 18-30°C with optimum growth at about 30°C, although some fruiting and flowering can occur at higher temperatures.^{24,36,64,78} Seed germination is influenced by temperature. The highest germination rates for widgeon grass seeds were observed to occur at temperatures of 25-28°C preceded by a cold stratification period (4-7°C) of several months.^{68,78,85}

Eelgrass

Water temperatures for eelgrass over its geographical range vary from 0-30°C.^{9,76,78} This temperature range is also reported for eelgrass distributions in Chesapeake Bay.⁸ Eelgrass grows slowly during the winter months of December through February with higher productivities in spring and fall and a decline in plant growth during summer.^{78,88} Eelgrass has a bimodal pattern of above ground growth with highest growth rates during spring and a second growth period during the fall.⁸ Temperatures above 30°C result in increasing respiratory losses of photosynthate which indicates that eelgrass is environmentally stressed.^{24,48,78} Four distinct, biologically determined seasons of eelgrass growth compared to the annual temperature cycle have been determined. The "winter" cycle is from 13°C to a low of 0°C followed by a warming trend to 9°C; "spring" from 9-23°C; "summer" from 23°C to a high of 30°C, followed by a cooling period to 25°C; and "fall" from 25-13°C.⁸

Eelgrass is a cold-water adapted species which grows best in the cool spring and fall months. Thus, it differs from most other Bay SAV species which have maximum productivity during the summer.⁷⁸

Salinity

All SAV are distributed mainly according to salinity concentrations conducive to growth. Most SAV species have little or no problem in tolerating decreased salinity, and it has been shown that enhancement of germination, growth and flowering often occur with a reduction in salinity.^{14,78,83} However, increases in salinity generally result in an overall growth reduction because plants expend energy in salt absorption to counteract increases in osmotic pressure rather than expending energy for growth.^{15,78}

Wild celery

In Chesapeake Bay wild celery generally has been considered to be restricted to the tidal fresh and oligohaline portions of the Upper Bay and tributaries.^{48,76,78} In early laboratory studies, wild celery could not be successfully maintained with salinity > 4.2 ppt,¹⁰ whereas others reported a threshold of 6.66 ppt.²⁸ More recently, laboratory evidence has shown a wider range in tolerance of wild celery to salinities from 0 ppt to 12 ppt.⁸³ Growth was unaffected by salinities up to 12 ppt, well within the mesohaline range.

Sago pondweed

Sago pondweed commonly is found in freshwater streams and ponds as well as brackish coastal waters.^{76,78} Maximum seed production, seed germination, and vegetative growth of sago pondweed has been reported to occur in fresh water. Tuber production and growth were stimulated at 3 ppt whereas at 8-9 ppt growth decreased and germination rates were decreased by 50%.^{76,78,79} Investigators have grown sago pondweed collected from fresh to brackish waters in laboratory cultures that varied from fresh to 9 ppt.^{40,86}

Redhead grass

Redhead grass occurs in oligohaline and mesohaline waters.^{76,78} Redhead grass has been reported to survive in salinities in the range of 5-25 ppt.^{2,76,78} However, redhead grass is generally found in localities of Chesapeake Bay where salinities are from about 1.5-19 ppt.⁷⁸

Widgeon grass

Widgeon grass is tolerant of an extremely broad range of salinity concentrations.^{22,78} In Chesapeake Bay, the upper limit for widgeon grass has been reported as both 30 ppt^{74,76,78} and 40 ppt;^{3,76,78} the lower limit of its salinity tolerance range is reported as 5 ppt.^{3,76,78}

Eelgrass

Eelgrass can tolerate salinities ranging from 8 ppt to polyhaline.^{4,5,49,61,62,76,78,82} In the York River, eelgrass generally does not grow upstream from areas where salinities are below about 10 ppt.^{8,54,76,78}

pH

In Chesapeake Bay, normal pH is from about 6 to 9. Most SAV species are able to tolerate a wide pH range, although drastic fluctuations could cause damage. Extreme pH values are unlikely, except perhaps locally, and therefore would have only localized effects on SAV.^{76,78}

The photosynthesis and respiratory activity of SAV causes diurnal fluctuations in the dissolved carbon dioxide content of the surrounding water which in turn affects pH. Therefore, as plants photosynthesize during the day and lower the dissolved carbon dioxide, pH will increase. At night when plants respire and give off carbon dioxide pH

will decrease.^{76,78} The pH, in turn, can affect plant enzyme activity, seed germination, and a variety of other plant responses. Plant enzymes exhibit optimum activity within specific pH ranges.^{71,76,78} The pH influences swelling of proteins and therefore is related to seed germination.^{76,78} Other plant responses such as heat susceptibility, enzyme solubility, and absorption of salts are affected by pH.^{20,76,78}

The median pH from a number of sago pondweed localities in central North America was 8.5.^{40,63} Sago pondweed has not been recorded in waters with pH < 6.3 and pH > 10.7.⁴⁰

The rate at which wild celery is capable of incorporating dissolved inorganic carbon, which is used in photosynthesis, declined by 61% with increasing pH from 7 to 8; whereas only slight changes occurred from pH 8 to 9.⁸¹ In contrast, wild celery plant weight, number of rosettes per plant, and plant buds have been reported to decrease with declining pH.⁴⁵ A review of the literature regarding ranges of pH and wild celery distributions showed that for most freshwater lakes and river systems from throughout the U.S. and Canada, pH ranged from about 6.5 to 9.2.⁴⁵

STRUCTURAL HABITAT REQUIREMENTS

Substrate

The distribution of submerged aquatic vegetation in Chesapeake Bay is dependent on the ability of the sediments to provide not only mechanical support for the plants, but also nutrients. In general, SAV are unable to grow in very coarse substrates (boulders, stones, and gravel) and occur in more stable sediments composed of sand or mud. Organic matter in the sediments leads to formation of anaerobic sediment which can enhance the availability of certain nutrients to SAV. However, too much organic matter can cause total oxygen depletion so that SAV growth is unlikely.^{76,78}

Wild Celery

Wild celery has been found to grow in a wide range of substrates. Early studies reported wild celery growing equally well in sandy sediment or mud.^{67,76,78} Others report wild celery only grew in sandy substrates in a Wisconsin Lake.^{46,76,78} Wild celery has also been reported growing in a variety of substrates that include gravel and hard clay but growing best in silty sand.^{31,45} A study examining wild celery growth in varying sediment types showed that wild celery thrived best in mixed sediment composed of about 48% silt, 21% sand, 14% clay, 9% gravel and 6.5% organics.^{34,76,78} Still others report wild celery growing in highly organic peat-like substrates.⁴⁵ In the Upper Chesapeake Bay most healthy beds of wild celery were found to grow in sandy-loam or sandy-silt sediments that consisted of at least 6% silt and between 1-5.3 % organic matter.⁸

Sago pondweed

Sago pondweed has been reported growing on a variety of substrates.⁷⁸ An extensive review of the literature showed sago pondweed growing in a number of different substrate types that include sand, silt, clay, loam, and organics. It was concluded that sago pondweed is not substrate-dependent and its distribution and abundance is a function of the water movement (i.e., wave action, fetch) which affects turbidity and the deposition of soft, easily colonizable sediments.⁴⁰

Redhead grass

A study of the substrate requirements for submersed plants in English Lakes showed that redhead grass grew best in moderately organic muds that were fairly rich in nitrogen and exchangeable calcium.^{52,76,78} Redhead grass has been reported to replace sago pondweed as sandy sediments became more fine textured.^{40,65}

Widgeon grass

In Chesapeake Bay widgeon grass has been reported growing on soft bottom muds, frequently on sandy substrates, and also growing in shallow ditches rich in organic muds.^{3,76,78}

Eelgrass

Eelgrass is found primarily on sandy substrates in Chesapeake Bay. The extensive rhizome growth of eelgrass can trap and bind sediments, providing some stability to the bottom substrate. This can result in a slight elevation of the eelgrass bed above the surrounding unvegetated substrate.^{56,76,78}

Current and Wave Action

Generally, SAV do not grow in areas of continuous strong currents or tides due to excessive scouring of the bottom substrates. Also, these are usually areas of increased turbidity from resuspension of fine sediment particles.^{76,78}

Wild celery

Wild celery is reported from waters with varying current and wave activity.^{30,45,78} Wild celery may tolerate high energy environments due to its wide leaf shape, basal meristem and root structure.^{30,35,45,78,80}

Transplants of wild celery in the Upper Chesapeake Bay were most successful when planted in areas protected from strong wave action.⁸

Sago Pondweed

Sago pondweed appears to do best in low to moderately turbulent areas. Sago pondweed has been reported as moderately tolerant of turbulence caused by wave action and even may be benefitted by the lack of potential macrophyte competitors at sites where water movement is substantial.⁴⁰ Seed production was reported highest in sheltered areas, whereas tuber production was at a max-

imum in high energy environments.^{41,78} Sago pondweed, unlike other SAV species, may have been able to persist during the damaging tropical storm Agnes in 1972 due to its lattice root structure.^{76,78}

Redhead grass

Redhead grass usually is found in still or standing waters.^{49,76,78}

Widgeon grass

Wave action can limit the growth of widgeon grass either through mechanical damage or by causing high turbidity.^{36,76,78} Its fragile branch tips at the water surface can be fractured by wave action and the broken off fragments are not able to survive.^{50,76,78}

Eelgrass

Along the eastern shore of the lower Chesapeake Bay eelgrass is reported growing behind offshore intertidal sand bars possibly due to protection for wave activity. In contrast, widgeon grass grows in the shallower waters on the bars suggesting that eelgrass is limited in its ability to withstand a combination of high temperatures and wave action.^{78,88} It has generally been recognized that eelgrass cannot compete well with other macrophytes along high energy shorelines.⁷⁵

SPECIAL PROBLEMS

Toxics

Toxics of concern to SAV include herbicides, heavy metals, and petroleum products. Herbicides are the most important and have been shown to cause negative impacts to SAV. Studies of heavy metal concentrations in SAV tissues have shown that no significant threat exists to either Chesapeake Bay SAV or consumers of SAV. Little data are available concerning toxic effects of petroleum on SAV.⁷⁸

The potential impact to SAV from herbicides in agricultural runoff has been an issue of concern in Chesapeake Bay since the dramatic SAV decline of the 1970's.^{76,78} It was noted that herbicide use had been increasing exponentially since their introduction in the 1960's.⁷⁷ Others suggested that the shift to chemical weed control was a possible cause for the SAV die-off observed in the Chesapeake Bay. Furthermore, it was postulated that increased herbicide use and in particular no-till (or minimum-till) agriculture might be especially detrimental to Chesapeake Bay SAV.¹⁸ More herbicides are required to control weeds with these farming methods than with conventional tillage.²⁷ Although the Baywide decline of SAV since has been attributed mainly to excessive loadings of nutrients and sediments,^{43,84} the potential for sporadic and localized damage to SAV from agricultural herbicides still must be addressed.

The majority of herbicides applied to agricultural fields in the Bay watershed are photosynthesis inhibitors with wide toxicity to many weed species. However, in aquatic environments, they have relatively fast degradation rates. There are some herbicide compounds developed specifically for aquatic weed control in freshwater ponds and lakes, but they too are relatively short-lived in the estuary.⁷⁸

Agricultural herbicides potentially can enter nearby waters through two mechanisms: leaching or dispersion into the dissolved portion of the water column and adhering to soil runoff particles. The concentrations of a given herbicide in runoff are dependent upon soil type and the specific herbicide characteristics, as well as application rate, land slope, and weather.^{76,78} For example, after monitoring runoff from a cornfield in the Rhode River watershed it was calculated that a 1.2% runoff loss of atrazine occurred in this silty loam soil type.⁹⁰ More recently, it was reported that out of five compounds applied to experimental watersheds in upper Chesapeake Bay, simazine had the highest concentrations in runoff with peaks in the range of 50-250 $\mu\text{g L}^{-1}$.^{73,78} Although there is increasing consensus concerning what levels of herbicides are toxic to SAV under estuarine conditions, it is still unknown to what extent sporadic herbicide runoff results in potentially lethal concentrations in the water column.⁷⁸

Early Chesapeake Bay SAV research examined the possibility that the commonly used agricultural herbicides (such as atrazine and linuron) were the primary factor responsible for the SAV decline of the 1970's. After extensive review of the literature it was concluded that herbicide concentrations in the field are seldom high enough to damage SAV populations. Furthermore, SAV recovery is rapid following exposure to low concentrations of herbicides, so even chronic exposure to the average concentrations found in the field would not produce permanent damage. Although periodic storm events which produce substantial herbicide runoff immediately following herbicide application could potentially have detrimental impacts on SAV, these would have local effects.^{76,78}

A recent analysis of sediments also supports the conclusion that in the field, herbicide concentrations are low. Six sites were analyzed for herbicide contamination in surficial sediments (upper 10 cm) in the upper, middle, and lower Bay regions. No detectable herbicide residues were found, lending further support to the conclusion that the Baywide SAV decline was driven predominantly by nutrient and sediment loadings.¹⁶ The possibility of herbicide toxicities still needs to be considered, however, when the adverse impacts of runoff on SAV cannot be explained by reduced light attenuation. Also, continued monitoring of runoff and its potential impacts to SAV is

necessary to assess whether new herbicide formulations could threaten remaining SAV.

The herbicide compounds most commonly used in the Chesapeake Bay watershed are atrazine, simazine, diaquat, paraquat, and linuron.^{76,78}

Atrazine and Simazine

Atrazine and simazine belong to the s-triazines and are the most widely used herbicides in the Bay watershed.⁷⁸ The s-triazines are absorbed readily to sediment particles in the water column. As these herbicide-laden particles settle, they may come into contact with SAV.⁷⁸ It was reported that soil-sorbed atrazine is relatively unavailable for plant uptake at concentrations as high as 120 $\mu\text{g/L}$, and that the shading effect of the soil particle itself poses a greater threat to SAV.³⁷ However, desorption from soil is rapid in the aquatic environment, so sediment concentrations on leaf surfaces are most likely in equilibrium with the water column and atrazine is readily taken up by plants from surrounding water.⁷⁸

Significant reductions in apparent oxygen production in estuarine microcosms containing SAV were observed following introduction of 0.13 mg/L atrazine. Surprisingly, oxygen production began recovering within two weeks of treatment; at four weeks it had returned to near pretreatment levels despite total atrazine levels remaining constant throughout the period.¹⁹

Therefore, although exposure to low concentrations of atrazine may cause an immediate reduction in SAV production rates, recovery appears to be fairly rapid especially if exposure time is short. This response is consistent with the findings of others.^{38,42,78}

Several studies have shown that the IC_{50} (the concentration at which photosynthesis and/or growth is reduced by 50%) for a number of Chesapeake Bay species is in the range 50-150 $\mu\text{g/L}$ for herbicides such as atrazine and simazine.^{18,21,38,39,42,78} An IC_{50} of 29 $\mu\text{g/L}$ is reported for sago pondweed.²⁵ The threshold concentration (the concentration at which photosynthetic inhibition is first observed) is about 20 $\mu\text{g/L}$.³⁹ Substantially higher IC_{50} values (474-1104 $\mu\text{g/L}$) have been reported when growth measurements such as leaf length and dry weight, which require longer term studies, have been used instead of photosynthetic response,²⁶ pointing out the possibly conservative nature of values obtained by short-term studies.⁷⁸

Furthermore, it has been reported that atrazine concentrations in excess of 10 $\mu\text{g/L}$ lasting over one day are relatively rare in Chesapeake Bay. Also, photosynthetic recovery of SAV is comparatively rapid at 10-25 $\mu\text{g/L}$ so that long-term declines in SAV from herbicide damage in the water column are unlikely. Therefore, low level dis-

solved concentrations (< 10 $\mu\text{g/L}$) atrazine are not widely viewed as major problems for SAV species in the Bay.^{38,78}

Linuron

In a manner similar to atrazine, linuron causes substantial reductions in SAV photosynthesis followed by photosynthetic recovery at initial concentrations of < 100 $\mu\text{g/L}$.⁴⁴ Unlike atrazine, however, the recovery is most likely due to herbicide degradation rather than detoxification. Recovery did not occur after exposure to concentrations of 500 and 1000 $\mu\text{g/L}$. Linuron appears to be slightly more toxic to SAV than atrazine, with slightly lower IC_{50} values. The maximum concentrations recorded in the estuary, however, are far below the IC_{50} indicating that this chemical is probably of limited significance to SAV in Chesapeake Bay.⁷⁸

Field sampling in several Chesapeake Bay estuaries indicated that linuron had been found at concentrations up to almost 9 mg/L in sediments.¹⁷ Bioassays showed that 1 mg/L linuron in sediments was sufficient to cause decreases in gross photosynthesis of another SAV species, horned pondweed.¹⁷

Diquat and Paraquat

These herbicides are used widely in no-till or minimum-till agriculture in Chesapeake Bay. Exposure to ultraviolet light (UV) normally causes photochemical breakdown of diquat and paraquat but since there is little UV penetration beyond the upper 1-2 cm of surface water, these herbicides are comparatively stable in aquatic environments.⁷⁸ However, since they are usually tightly absorbed to clays, they present minimal problems to plant life.

Other Environmental Factors

Potential damage to SAV can occur from other environmental factors such as intensive foraging by wildlife, boat traffic, dredging, and shoreline development. Although these activities by themselves are not responsible for the current reduced levels of SAV Baywide, they can negatively impact SAV on a local level.

Foraging

Fauna, including carp, cownose rays, and waterfowl, may destroy SAV. Carp cause destruction to SAV by their foraging activities for mollusks and crustaceans in the soft mud. The SAV beds are damaged directly by the physical uprooting of the plants and indirectly by the exclusion of light due to the turbid waters and floating plant fragments.^{49,70,76,78}

Cownose rays have also been documented to cause damage to SAV beds by their feeding activities. Large patches of eelgrass beds in the lower Chesapeake Bay have been uprooted by cownose rays digging with their pectoral fins in search of bivalve mollusks.^{55,76,78}

Waterfowl are well known for their food preference for SAV. Fluctuations of waterfowl populations have been reported to cycle with SAV fluctuations. In fact, the decline in SAV distribution and abundance has been attributed as a primary cause for the reduction in Bay waterfowl populations.^{53,76,78}

Boat Traffic

Damage to SAV from boat traffic has been of local importance. Direct damage to plant beds occurs from boat propellers. With the increased numbers of registered boats using the Bay, the potential for damage to remaining SAV could be more extensive.⁷⁸

Dredging

Clam dredging causes damage to SAV by physically uprooting the vegetation and by increasing turbidity in the surrounding area. Historic levels of clam dredging in Chesapeake Bay were not considered as having any long-term impact to Baywide SAV distribution and abundance.^{76,78} With recent declines in other Bay fisheries resources clamming activities have increased, which may present a greater potential for negative impacts to remaining SAV populations.

Dredging for channel maintenance also directly damages SAV by removing the vegetation and altering the habitat (i.e., increased depth) usually prohibiting SAV from recolonizing the area due to insufficient light in the deeper water. Also, increased turbidity from the dredging activity can negatively impact SAV in surrounding areas.^{76,78}

Shoreline Development

Shoreline development activities such as marinas and construction of waterfront properties can negatively impact any remaining SAV beds. Also, this development can result in the loss of shallow water habitat which may reduce potential habitat that SAV could recolonize following improved water quality.

RECOMMENDATIONS

Recommendations for improving habitat conditions necessary for SAV to successfully grow and reproduce include:

Reduction of sediments and nutrient loadings

The Baywide decline of SAV has been attributed to excessive loadings of sediment and nutrients from the surrounding watershed. Federal, state, and local management agencies throughout the Bay drainage basin should continue efforts to reduce loadings of these pollutants through point source and non-point source control programs.

Setting habitat requirements as regional goals

The habitat requirements identified as critical for successful SAV growth should be minimum regional goals for improving water quality. Additional water quality monitoring may be necessary to measure success in achieving these regional goals.

Refine habitat requirements

Research must continue to further refine the habitat requirements for SAV. The habitat requirements for SAV identified in this document and the *Chesapeake Bay Submerged Aquatic Vegetation Habitat and Restoration Goals: A Technical Synthesis*⁸ are the minimum levels necessary for establishment and maintenance of current SAV populations, not for guaranteeing conditions for restoration of depleted SAV populations.

Continue Baywide monitoring of SAV

Baywide monitoring of SAV distribution and abundance should continue to provide a measure of the success of restoration efforts aimed at improving water quality. SAV has been shown to be relatively responsive to changes in water quality. Also, unlike other living resources, SAV can be efficiently monitored to provide an accurate account of Baywide distribution and abundance through use of aerial and ground surveys.

Protect remaining SAV and potential SAV habitat

Protection of remaining SAV populations as well as potential shallow water SAV habitat areas, should be given a high priority. Damage to remaining SAV beds for example, from dredging and construction activities, should be avoided. Potential shallow water habitat as defined in the *Chesapeake Bay Submerged Aquatic Vegetation Habitat and Restoration Goals: A Technical Synthesis*⁸ is based on historic distribution data and the 2 m depth contour of the Bay and its tidal tributaries. These areas are also in need of protection to provide SAV with additional habitat that could be revegetated following improved water quality. Revegetation of these areas would contribute to restoration of SAV acreage and abundance throughout the Bay.

Continue to monitor other factors

Other environmental factors such as herbicide loadings, dredging, and boat activities have been shown to impact SAV. These types of activities tend to be local in nature and, by themselves, have not caused the current Baywide reduced levels of SAV. However, the low remaining SAV populations may not have the resiliency of former distributions and densities, and thus be less able to withstand the impacts from these activities, especially at greater intensities.

CONCLUSIONS

SAV is a key component of the Chesapeake Bay ecosystem. Baywide distribution and abundance of SAV has undergone a severe decline in recent decades mainly due to excessive loadings of nutrients and sediments. Key habitat requirement parameters have been identified and the threshold levels of these parameters necessary to establish and maintain SAV populations have been determined. Furthermore, other environmental factors that pose potential threats to SAV are known. To ensure that remaining SAV distribution and abundance experience no further reductions, protection of these populations should be given priority. Furthermore, if SAV distribution and abundance are to improve to former historic levels, exces-

sive nutrient and sediment loading must be reduced and the threshold levels of the key habitat parameters must be met.

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Table 1. Summary of Chesapeake Bay SAV habitat requirements by region as proposed in Batiuk *et al.*⁸
 DIN = dissolved inorganic nitrogen; DIP = dissolved inorganic phosphorus; Chl *a* = Chlorophyll *a*;
 TSS = total suspended solids.

REGION	SALINITY/ SPECIES	DIN mgL ⁻¹	DIP mgL ⁻¹	Chl <i>a</i> µgL ⁻¹	Light Attenuation m ⁻¹	Secchi Depth m	TSS mgL ⁻¹
UPPER BAY	Tidal Fresh/ Oligohaline (wild celery, sago pondweed)	NRE ^a	< 0.02 necessary for SAV survival; > 0.02 leads to declines of marginal SAV beds.	< 15	< 2	> 0.8 in sheltered areas; > 1.0 in unsheltered	< 15 No SAV found in areas > 20; healthy SAV beds in areas < 10
POTOMAC RIVER	Tidal Fresh (wild celery)	NRE ^b	≤ 0.04 correlated with SAV revegetation	≤ 15	≤ 2.2 for revegetation and increased abundance	≥ 0.5 for SAV to survive; ≥ 0.7 necessary for revegetation	≤ 15-16 for expansion and revegetation
	Oligohaline (wild celery, sago pondweed)	NRE ^c	≤ 0.04-0.07 correlated with survival of established SAV beds and revegetation	≤ 15	< 2.7 for previously established SAV beds	≥ 0.5	< 20 for maintenance of existing populations
MIDDLE BAY/ CHOPTANK RIVER	Mesohaline (sago pondweed, redhead grass, widgeon grass)	< 0.15	< 0.01	< 15 SAV survived; < 10 to sustain populations	< 1.5 for abundant SAV growth; < 2 for survival of marginal SAV growth	> 0.8	< 15
LOWER BAY/ YORK RIVER	Polyhaline (widgeon grass, eelgrass).	< 0.15	< 0.02	< 15	< 1.5	> 0.8	< 15

a. No Requirement Established (NRE). No DIN habitat requirement could be established because of inconclusive data.

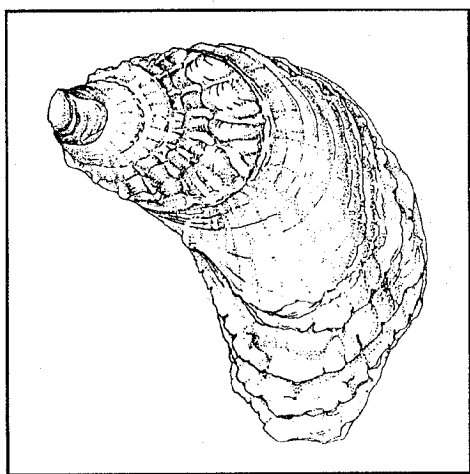
b. No DIN habitat requirement could be established. Ammonia concentrations ≤ 0.4 mgL⁻¹ were associated with SAV revegetation and ammonia concentrations > 0.6 mgL⁻¹ were associated with revegetation failure. Nitrate plus nitrite concentrations ≤ 1.7 - 2 mgL⁻¹ were associated with SAV propagation and survival.

c. No DIN habitat requirement could be established. SAV survival occurred at ammonia concentration 0.4-0.7 mgL⁻¹. Nitrate plus nitrite concentrations ≤ 1.7 - 2 mgL⁻¹ were associated with SAV propagation and survival.

EASTERN OYSTER

Crassostrea virginica

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The eastern oyster is a resilient estuarine species that is well adapted to its fluctuating environment in the Chesapeake Bay. It tolerates wide natural variation in temperature, salinity, suspended sediments, and dissolved oxygen, to the extent that environmental regulations protecting more active or more sensitive species like blue crabs and striped bass will probably protect oysters. It is fecund enough to produce billions of spat in the Bay if brood stock abundance is high, suitable hard substrate is plentiful, and climatic conditions are optimal. Predation causes high mortality of the young stages. High mortality rates also have been caused by diseases in recent years. Pollution is a local problem for oysters near industrialized regions of the Bay. Overfishing has led to depressed harvests, degraded oyster grounds, and a weakened fishery. To rehabilitate the resource, it will be necessary to understand aspects of oyster biology more completely (especially diseases), to rehabilitate the oyster grounds, to manage the

resource according to scientific principles, and to encourage the growth of aquaculture.

INTRODUCTION

The eastern oyster is a very fecund commercial bivalve that is well-adapted to an estuarine existence. Consequently, it is very resistant to the wide swings of temperature, salinity, turbidity, and dissolved oxygen that characterize its habitat. In addition to its fecundity, the species has morphological, physiological, and behavioral adaptations that, by colonial times, allowed it to persist in immense numbers in the Chesapeake Bay. European settlers reported that cemented agglomerations of oyster shells formed navigational hazards ("rocks") thrusting up from the soft Bay bottom.

The filtering activities of these massive concentrations of oysters may have resulted in the Bay harboring a much different assemblage of phytoplankton and zooplankton than at present. This assemblage may have contained fewer sea nettles, microplankton, and bacterioplankton, and the Bay waters probably were much less turbid than

now, thus allowing submerged aquatic vegetation to thrive.

Naturally, these immense beds of oysters began to be exploited by early settlers, to the extent that the Bay fishery was one of the most important in the U.S. at the turn of the 20th century.⁴³ However, politically directed management of the Bay's oyster resources at the behest of oyster harvesters resulted in virtually unregulated overharvesting and subsequent decline in the abundance of the species over the past century. In some heavily populated regions of the Bay, pollution and high sediment loads have also contributed to the decline. Oyster beds in unpolluted or relatively unpolluted regions (roughly from Eastern Bay south on the Eastern Shore, and in the Patuxent and Potomac River mouths on the Western Shore, with scattered populations elsewhere) are in danger of being overwhelmed by sediment because overfishing has led to excessive scraping of the substrate, leaving the surface of the beds projecting just above the sediment where it can be covered during storms.

The repeated warnings of numerous scientists and commissions of inquiry and their recommendations for conservation of the resource have generally been ignored by the Maryland and Virginia legislatures.^{43,44} Oyster farming (aquaculture) in Maryland has been discouraged for most of the 20th Century by passage of various laws. The potential for rehabilitation of the fishery has been greatly hindered by episodic incidences of lethal diseases over the past 30 years.

With over-exploitation and disease having depleted oyster stocks, the Bay fishery is a fraction of what it once was. Over 15 recent years (1971-1986), oysters have represented 21% of Maryland's total commercial fishery catch and 48% of dockside value. However, from 1983 to 1986, these proportions declined to 8% and 30%, respectively.⁸ Catches have declined dramatically from 14 million bushels in 1890 shortly after overfishing began to less than 0.5 million bushels per year since 1987. The market for Bay oysters has declined along with the harvest, so that an increasing market share has been captured by aquaculture industries on the Pacific coast of the United States and elsewhere.

Because it is highly adapted for an estuarine existence, and because the central Chesapeake Bay is so conducive to sustained reproduction, settlement, and growth of oysters, the eastern oyster could once again become a major natural resource in the Bay if aquaculture were encouraged and if resources were available to rebuild oyster beds in formerly highly productive habitat. The oyster is immobile for much of its life, and therefore does not have a high metabolic demand. As will be described later, it is resistant to all but the most extreme environmental fluctuations. Consequently, except perhaps for anthropogenic chemicals found near industrial population centers, water quality criteria established for more metabolically active and sensitive species such as the blue crab and the striped bass will undoubtedly protect the oyster as well.

BACKGROUND

The eastern oyster, also known as the American oyster or Virginia oyster, is a bivalve mollusk in the family Ostreidae, a family that is worldwide in distribution, and that supports numerous commercial fisheries in many nations. The eastern oyster ranges along the coast of North America from the Gulf of St. Lawrence to the Gulf of Mexico. It has been introduced to Hawaii, the west coast of North America, and other locations worldwide. Its typical habitats are estuaries, sounds, and bays, from brackish water to hypersaline lagoons. It is found in the shallows of the Chesapeake Bay from salinities above about 5 ppt in the upper Bay and its tributaries to the near-oceanic salinities of the Bay mouth.

Four recent reviews of oysters in general and the eastern oyster in particular are the authority for statements in this text, unless otherwise noted.^{2,33,44,48}

LIFE HISTORY

Reproduction

Adult oysters are immobile, but release eggs and sperm into the water where external fertilization occurs. Production of spawn (gametogenesis) depends on storage of glycogen, which begins after spawning in summer or autumn with the accumulation of nutrients and which slows or stops under winter conditions. Ripening (development of gametes) is rapid (over a few weeks in the Chesapeake Bay) as water temperatures warm above 10°C in spring. Temperature increase stimulates natural spawning, and spawning in the Bay may occur at 18°C (limited spawning) to 20°C and above.⁴⁵ The presence of sperm or eggs also stimulates release of gametes, as may the presence of some chemical (perhaps food-related) in the water pumped by adults.^{45,93} Where temperatures permit, females may spawn more than once in a season, with up to 20 million eggs (sometimes more) released at any one time by an individual female, depending upon her size and condition.

Larval Development and Settlement

Fertilized eggs develop into ciliated veliger (D-stage, straight-hinge) larvae in 24 hours or less, depending upon temperature. During the next two to three weeks the free-swimming larva grows until ready to settle. Before settlement occurs at about 260-300 µm, a foot develops (pediveliger stage). The foot is used to crawl and "explore" substrate before settlement and metamorphosis occurs. When a suitable substrate is found, liquid cement is extruded from a pore in the foot and the left valve becomes fixed in place. Subsequently the ciliated velum that allowed the larva to swim is discarded, the foot is reabsorbed rapidly, and gills and a digestive tract are elaborated. The attached juvenile oyster is called a spat.

Metamorphosis will be delayed if suitable substrate is unavailable (e.g., as a result of siltation, presence of noxious chemicals, etc.). The length of delay that can occur in nature is unknown, but Coon *et al.*¹⁸ have been able to keep competent-to-settle Pacific oyster (*Crassostrea gigas*) larvae in the laboratory for 30 days without settlement occurring. Settlement and metamorphosis in the eastern oyster are mediated by neuroactive compounds such as L-3,4-dihydroxyphenylalanine (L-DOPA), epinephrine, and norepinephrine.^{16,17} Anthropogenic substances in the water column that mimic or inhibit such compounds might stimulate settlement prematurely or inhibit it, but this possibility has not been explored at all.

The planktonic larval stage is the only mobile stage. Larvae can swim up or down in the water column, but are

carried more-or-less passively by horizontal water movements.

Growth

Fastest relative growth occurs in the early months of an oyster's life. Annual growth rate is affected by temperature (the rate increases from north to south), by food quality and quantity, by salinity, and by parasitic infection. Shell growth may be greatest in spring as water warms. Growth of the soft body tissues is greatest after spawning ends, as glycolytic reserves are built up in preparation for gametogenesis during the subsequent winter. Growth slows in the spawning season as energy is allocated to production of eggs and sperm.

ECOLOGICAL ROLE

Substrate

Because estuaries are areas of high sediment deposition, their basins are predominantly soft-sediment in nature, subject to continual sediment influx from the surrounding watersheds. As a result of its production of shell, the eastern oyster provides the greatest volume of hard substrate found in estuaries. In pristine or carefully managed habitats, oyster reefs can be massive, thus affording extensive attachment area for oyster larvae, as well as numerous associated species that, like oysters, require solid substrate. As a result of overfishing in the Chesapeake Bay, oyster shell substrate is usually limited to a relatively thin layer of dead shell and live oysters spread widely over Bay bottom. These damaged habitats are more readily covered by sediment because currents are slower near the bottom. In addition, reefs with many live oysters seem to remain freer of sediment for reasons that are not clear but may include the effects of water pumping and vigorous shell clapping by the resident oysters. Ultimately, over-exploited reefs disappear, overwhelmed by sediment, leaving less habitat available for oysters and other species that require hard substrate, such as hooked mussels, tunicates, bryozoans, and barnacles.

Principal Foods

As is characteristic of a species with planktotrophic larvae that depend on phytoplankton for food, oyster eggs are supplied with the minimum lipid reserves to support energy requirements until feeding and digestive systems develop and function. For the 2-3 weeks of larval existence before settlement, suitable planktonic food is necessary for survival and metamorphosis. Young spat grow rapidly after settlement and have low food reserves; an adequate quantity and quality of phytoplankton is required for the buildup of nutrient reserves to meet metabolic needs over winter. The adult also requires suitable food to support gametogenesis. Preliminary data on studies in the Choptank River indicate that Broad Creek and the Tred Avon River have sufficient food to support the presumed food requirements of any life history stage

of the eastern oyster (personal communication: R. Newell, Horn Point Environmental Laboratory).

Larvae, spat, and adults ingest predominantly living plankton. Oyster larvae can ingest food particles ranging in size from 0.2 to 30 μm , selectively ingesting 20-30 μm organisms.⁴ Adults are less efficient in retaining particles below 3 μm in diameter than in retaining larger particles.⁵⁰ The biochemical composition of algal cells as well as cell size is important. The detrital complex in the seston appears to supply very little of an adult oyster's carbon requirements in Maryland's Chesapeake Bay.^{19,74}

Role as a Filter Feeder

Recently, it has been proposed that over-exploitation of oysters in the Chesapeake Bay has reduced the important filtering role oysters play in the ecosystem, resulting in major biotic changes.⁷³ Oyster populations in the Bay are calculated to have declined since the late 19th century from a standing stock biomass of 188 million kg dry tissue to a present biomass of 1.9 million kg dry tissue. Where once the population in summer was capable of filtering the Bay's entire water column from surface to bottom in an estimated 3 to 6 days, present stocks require an estimated 325 days. The pre-1870 oyster population is estimated to have been capable of filtering 42-77% of the 1982 daily carbon production in Bay waters shallower than 9 m, compared with less than 1% filtered by the 1988 population.⁷³

Newell⁷³ hypothesized that the loss of such a major filtering assemblage may have been an important factor in the apparent shift to microbial food webs in the Bay and to an increase in zooplankton, including gelatinous zooplankton (ctenophores and jellyfish). Restoration of oyster populations by aquaculture and the careful management of public beds would improve water quality through the enhanced removal of particulate carbon by oysters. Oyster biomass would then be harvested, permanently removing the carbon from the system. Note also that many of the organisms commonly found attached to oyster shells (e.g., hooked mussels, tunicates) are also filter feeders whose numbers may also have declined as a consequence of the decline in oyster populations.

Predation

The oyster, like all bivalves that broadcast sperm and eggs into the water column, suffers over 99% loss of gametes, fertilized eggs, and larval stages before settlement occurs. Much of that loss is undoubtedly due to predation by ctenophores and other planktivores. Benthic carnivores that consume oyster larvae include sea anemones, the scyphistoma stage of sea nettles, and probably a variety of filter feeding invertebrates. Newly settled spat are consumed by the carnivorous flatworm *Stylochus ellipticus*, and by small crabs. Older spat and first year oysters may be eaten by larger blue crabs and some fish. In higher

salinity waters (>20 ppt), predatory snails and starfish feed on oysters, including the largest individuals. Finally, disease kills many oysters, usually those older than one year; salinities below about 12 ppt seem to protect oysters from disease. Water saltier than about 5 ppt is excellent habitat for oyster production because predatory snails and starfish are generally absent, with disease limited in low salinity years.

HABITAT REQUIREMENTS

A number of "physiological races" of the eastern oyster apparently exist along the western Atlantic coast.^{54,55,56,94} These races appear to differ in timing of gametogenesis and spawning as a function of geographic location and temperature regime. Studies are currently being conducted on these differences. Relatively few data on environmental requirements of the eastern oyster have been collected from Chesapeake Bay populations. Existing data have been collected as the result of experiments in Long Island Sound, Delaware Bay, and the Gulf of Mexico, so they may not be entirely accurate for Bay oysters. But these data do provide general insights into tolerances and adaptations of the eastern oyster. Table 1 summarizes habitat requirements for temperature, salinity, sediment, pH, and dissolved oxygen. These requirements are "best estimates" rather than exact values, but can serve as guides for managers.

Water Quality

Temperature

Temperature influences growth, development, reproduction, and feeding activity. It has not been reported to jeopardize oyster populations, except where industrial discharges release much warmer water than occurs naturally. Oysters cannot control their body temperature, and are subject to a temperature range of about -1°C to about 36°C throughout their geographic range. Oysters exposed to air at low tide in southern regions have briefly attained body temperatures of 46-49°C.³³ However, temperatures much above about 32°C would be stressful over a period of many hours or days and could be lethal in winter when oysters are acclimatized to cold temperatures.

The eastern oyster has a maximum rate of ciliary activity (responsible for pumping water for respiration and feeding) at about 24-26°C. Ciliary activity is usually disrupted above 32°C and feeding may cease below 6-7°C.^{33,52,70}

Efforts to determine lethal temperatures by Henderson³⁷ and Fingerman and Fairbanks³⁰ were environmentally unrealistic and did not produce data that are ecologically useful. No other studies on lethal temperatures of adults or spat have been reported. However, to simulate conditions of passage through power plant cooling condensers, Hidu *et al.*⁴⁰ subjected fertilized eggs, ciliated gastrulae,

and 2-day-old veliger larvae to temperature increases for periods from 10 seconds to 16 hours. Mortality increased with increasing temperature and exposure time. Fertilized eggs were least resistant to higher temperatures, followed by ciliated gastrulae, then veliger larvae. Maryland law governing temperature addition to estuaries should protect oysters from lethally high temperatures, and heated effluents are not allowed near oyster beds.

Temperature affects rate of larval development. In the Bideford River, Canada, oyster larvae required 30 days to reach 365 µm in length at 19°C, 26 days at 20°C, and 24 days at 21°C.⁶⁷ Maximum larval growth in the laboratory occurred between 30.0 and 32.5°C at Long Island Sound salinities between 10.0 and 27.5 ppt²², and larvae reached setting stage in 10-12 days at 30-32.5°C and 36-40 days at 20°C. Diaz²⁶ noted that a five-second exposure to a 20°C increase above 25°C (but not increases of 10 or 15°C) permanently impaired larval growth; his results would be applicable to larvae exposed to industrially heated water.

Increased temperatures (below lethal levels) influence setting success of pediveligers. In the Delaware Bay, an increase in temperature from 24 to 29°C for four hours increased the percentage of larvae that set.⁵⁹ Such temperature increases occur when water floods over tidal flats heated by exposure during ebb tide. Setting in Virginia was also found to be influenced by the age of larvae and degree of temperature increase above 25°C.⁴⁰

Salinity

Like temperature, salinity influences growth, development, reproduction, and feeding activity. Oysters tolerate a wide range of salinities and thrive in the mesohaline waters of Chesapeake Bay; they become less abundant toward the head of the Bay and in the upper regions of Bay tributaries where salinity falls below about 5 ppt. The most deleterious salinities are low salinities associated with freshwater flooding over a number of weeks.

Low salinity can be fatal, and can inhibit feeding, growth, and spawning. In an extensive study by Loosanoff,⁵¹ there were no differences in salinity tolerance among oysters of different ages, including spat. Oysters could feed at levels as low as 5 ppt if temperatures were cool, but no feeding was ever observed at 3 ppt or below. The crystalline style disappeared in oysters held in low salinities (a sign that feeding was not occurring) but regeneration occurred soon after the oysters were returned to normal salinities. Growth was limited or nonexistent at 5 ppt or less, retarded at 7 ppt, and unaffected at 12 ppt and above.

Salinities of 0 and 3 ppt totally inhibited gametogenesis in Loosanoff's experiments.⁵¹ At 5 ppt, gametogenesis was arrested in about 50% of an experimental sample, and depressed in the remainder of the sample. At 10 ppt, 12 ppt, and 27 ppt (control), oysters were ripe, with some

starting to spawn. If oysters were held in ambient conditions and allowed to grow until the gonads began enlarging (about three weeks before the normal onset of spawning) and were then placed in lower salinities, 0 to 5 ppt inhibited further gonad development. Normal gametogenesis proceeded at 7.5 ppt and above, with some oysters spawning at 7.5 ppt and with more intense spawning in higher salinities. Salinities of 7.5 ppt or above are necessary for gametogenesis and spawning to be even moderately successful.

Pumping rate (method of assessment not stated by Loosanoff)⁵¹ was strongly affected by sharp reductions of salinity from 27 ppt (control) but began to increase somewhat after additional exposure (acclimation) to the lower salinities. Rapid changes from low to high salinities had little effect. Oysters accustomed to living in lower salinities were more tolerant of the effects of even lower salinity (as measured by shell-closing behavior or by pumping behavior) than were oysters used to living in higher salinities.⁵¹

Optimum salinity and the salinity range for the development of oyster eggs into straight-hinge larvae is influenced by the salinity experienced by the parents during gametogenesis.²¹ Thus, adults acclimated at 26.0-27.9 ppt produced zygotes that developed over a salinity range of 12.5-35 ppt, with an optimal development at about 22.5 ppt. Parents acclimated to about 9 ppt produced zygotes that developed within a range of 7.5-22.5 ppt with optimal development between 10.0-15.0 ppt. Optimal larval growth occurred at 17.5 ppt for larvae whose parents were held at 26.0-27.9 ppt. Thus, optimal salinity conditions for larval development will differ with location in the Chesapeake Bay.

For older larvae (165 μ m long) from parents acclimated to 26.0-27.0 ppt, Davis²¹ found good growth between 12.5 and 17.5 ppt and in the controls (26.0-27.0 ppt), and limited growth at 7.5 ppt (25% of control value). Setting was good between 12.5 and 17.5 ppt but non-existent at 7.5 ppt. No experiments were made with larvae from parents held in low salinity conditions.

Davis²¹ speculated that oyster populations in low salinity areas (< 10 ppt) may depend on the influx and settlement of nearly full-grown larvae from higher salinity areas. In upper Chesapeake Bay, Eastern Bay and the lower Choptank River are the northernmost regions with consistently good spat settlement success. Both these areas have salinities generally above 10 ppt during the spat settlement period, in contrast with the less saline Chester River further up the Bay which is not usually self-supporting in terms of spat settlement. Setting of oyster spat in the Bay varies directly with the cumulative high salinity during the spawning season in the central Bay.⁹⁷

When Chanley¹⁵ placed recently set spat (0.3-0.5 mm long) directly into salinities ranging from 2.5 ppt to "full salinity" (not specified) at 21-24°C, 100% died within two weeks at 2.5 ppt and 50% died at 5 ppt. Growth at 7.5 and 10.0 ppt was slow compared to growth in higher salinities. In a second experiment, spat (1.0-1.4 mm) that were transferred gradually to experimental conditions over a week experienced poor growth at 10.0 and 12.5 ppt and least growth at 7.5 and 5.0 ppt. At 2.5 ppt, only 19% survived, compared with 66% at 5 ppt and 80-100% at the remaining salinities.

Based on these studies^{15,21,51} one can expect larvae to grow well at about 12.5 ppt and higher whereas spat and adults should grow slowly from about 7 to 12 ppt and normally from 12-27 ppt.

Responses of different life history stages of oysters to salinity vary with temperature. For example, mortality in oysters subjected to fresh water and low salinities increases as temperature increases.⁵¹ Salinity also affects temperature tolerance of oyster larvae.²² At salinities from 10.0 to 27.5 ppt, the optimum temperature for larval growth was between 30.0 and 32.5°C, but was 27.5°C at 7.5 ppt. No well-defined optimum growth salinity was delineated; growth depended upon the experimental temperature. Reduced salinities reduced the temperature range that eggs and larvae could tolerate for development and growth.

Managers should understand that there is a synergism between temperature and salinity in relation to their effects on oysters. However, temperature regulations in Maryland seem adequate to protect oysters, and no salinity regulations seem to be required.

Suspended Sediments

The eastern oyster is well adapted to withstand erratic environmental increases in turbidity and sedimentation resulting from the effects of wind, currents, runoff from land, etc.⁶⁸ Most studies of sediment effects on the eastern oyster have involved sediment concentrations that are higher than usually encountered in nature.

Nelson⁶⁹ found the oyster to be capable of feeding rapidly in waters containing up to 0.4 g (dry weight) of suspended matter per liter. He described the efficient gill filtration system that allows for this, including the promyal chamber which is characteristic of oviparous oysters (genus *Crasostrea*), and concluded that the oyster (at least from turbid Delaware Bay) is able to feed in the presence of heavy loads of suspended sediment.^{71,72} However, oysters from less turbid Long Island Sound are more sensitive to high sediment concentrations.^{53,58}

Loosanoff and Tommers⁵⁸ provided quantitative estimates of pumping rates by oysters from Long Island Sound in

the presence of various concentrations of turbidity-creating substances. Feeding was most efficient when the water contained little suspended material. Additional studies reported by Loosanoff⁵³ showed that even for short exposures (3-6 hours), oysters demonstrated sensitivity to a variety of particulate materials. As particle concentration increased, the rate of water pumping dropped, reaching zero in high concentrations of suspended material. Upon return to clean sea water, oysters exposed for longer periods took longer to recover than oysters held in the same sediment concentrations for shorter periods. Loosanoff⁵³ assumed that the longer exposure period resulted in tissue damage to the filtering apparatus.

Oyster eggs and larvae can be killed by suspended sediment.²³ Concentrations of 0.25 gL⁻¹ resulted in 27% mortality, with 69% mortality at 0.5 gL⁻¹, and 97-100% mortality from 1 gL⁻¹ and above. Davis and Hidu²³ concluded tentatively that larger particles were primarily responsible for the mortalities. Larvae were more tolerant of sediment than were eggs. A concentration of 0.5 gL⁻¹ of sediment led to nearly 20% mortality in eastern oyster larvae after 12 days of exposure,²³ with 50% mortality between 1.0 and 1.5 gL⁻¹ and 100% mortality at 3 gL⁻¹. Eastern oyster larvae suffered reduction in growth in 0.75 gL⁻¹ of sediment, and growth stopped at 2 gL⁻¹. To place their results in an environmental perspective, Davis and Hidu²³ noted that eastern oyster larvae tolerated experimental turbidity levels higher than those normally encountered in nature. However, they felt that excessive turbidity caused by storms or activities such as dredging might be detrimental to oysters.

Dissolved Oxygen

Although limited experiments have been performed to evaluate the effects of low dissolved oxygen on oysters (whether measured in terms of survival, physiological activity, reproduction, or spat settlement) the eastern oyster seems to be a tolerant species. It is an oxygen regulator down to a critical oxygen tension of about 30 mm Hg at 20°C and 28 ppt.⁸⁸ Below 30 mm Hg, it becomes an oxygen conformer. Louisiana oysters (30-50 mm long) starved for 35-65 days remained resistant to anoxia, with their metabolic rate depressed to only 75% of the normoxic rate.⁹⁵ Values of LT₅₀ (days of exposure to anoxia causing 50% mortality) for these oysters when held at salinities of 10, 20 and 30 ppt were 28 days at 10°C, 18-20 days at 20°C, and 3-8 days at 30°C.⁹⁵ Compared with blue crabs (29-54 mm carapace width) from the same region, oysters were much more resistant to hypoxia and anoxia, both in terms of metabolic rate and of mortality.

Elsewhere, oysters have survived for up to 5 days (no temperature data given) in water containing less than 1.0 mgL⁻¹ oxygen.⁹¹ Presumably they underwent anaerobic metabolism during that time.³³ Median mortality times for anoxia-exposed larvae are 11 hours for 82 µm larvae and

150 hours for 16 mm spat.⁹⁹ Kennedy (personal observations) found that larval swimming rates after 12 hours at oxygen concentrations as low as 0.5 mgL⁻¹ were not significantly different from rates at saturation levels of oxygen. Also, oyster larvae avoided low oxygen water (exposure to about 1 mgL⁻¹ or less for one hour) by swimming upwards, an action that would bring them towards the surface where hypoxia is minimal.

Because of larval avoidance of hypoxia, and spat and adult resistance to low dissolved oxygen concentrations, short-term (days) intrusions of anoxic and hypoxic waters over shallow (<5-10 m) oyster beds are probably not deleterious. Should such intrusions kill less tolerant shell-fouling organisms, space would become available on the oyster shell for settlement by larvae. Regulations designed to protect blue crabs from low dissolved oxygen would serve to protect the oyster as well.

pH

Estuaries are generally well-buffered systems, with pH in unpolluted waters ranging from 6.8 to 9.25, depending upon time of day and season. Data on pH tolerances of oysters are meager. Oysters were found to spawn at pH 7.8 to 8.2 in Long Island Sound,⁷⁹ and not below pH 6.0 or above pH 10.¹³ Pumping rate in adults was normal at pH 4.4, but oysters at pH 4.25 remained open about 76% of the time and pumped about 90% less water than did controls at pH 7.75.⁵⁷ At pH 6.75 and 7.00, oysters initially pumped more than did the controls at 7.75, but the rate gradually declined to become less than in the controls.⁵⁷ Respiration is also affected by pH; at pH 6.5, oxygen consumption was 50% of normal, decreasing to 10% at pH 5.5.³³

Normal embryonic development occurs at pH 6.75 to 8.75.¹² Survival of larvae was more than 68% in the range of 6.25 to 8.75, with pH 6.00 being the lower limit for survival. Normal larval growth occurred from pH 6.75 to 8.75, with growth dropping rapidly below pH 6.75. Abnormal development of eggs and mortality of larvae increased rapidly at pH 9.00 to 9.50. Calabrese and Davis¹² concluded that successful recruitment of oysters requires a pH above 6.75. High concentrations of sediment lower seawater pH below 6.75 to 6.40. Thus, heavy sediment loads (or any pollutant lowering pH in tidal estuaries) may lead to failure of oyster recruitment.

Structural Habitat

Substrate

Even with an efficient mechanism for tolerating the often heavy sediment load in estuaries, oysters can be overwhelmed and buried by heavy sedimentation,⁷² with death by suffocation resulting. In general, oysters survive best on bottoms that are firm, such as those of shell, rock, and firm or sticky mud. Sand bottoms are subject to shifting activity, resulting in abrasion and valve injury. In

addition, shifting sand destroys young spat of the flat oyster, *Ostrea edulis*,⁸⁵ so presumably young eastern oyster spat would also be at risk in sandy environments.

Oyster shell is the most suitable substrate for spat settlement. The removal of whole oysters from the Bay and their transport to distant markets means that there is a constant drain of this cultch from the Bay. Alternatives such as buried shell are in finite supply, so if shell conservation is not practiced or if replacement material is not readily available, future spat settlement will be hindered.

Depth

In years past, oysters were dredged from the deeper waters of the Bay by sailboats, but most beds now are found in the shallows along the shore and in Bay tributaries where sediments are firmer and where the supply of dissolved oxygen is more reliable.

SPECIAL PROBLEMS

Overfishing

For the past century, management of the Bay's oyster industry has been influenced predominantly by political concerns rather than by scientific information.⁴³ The result has been a steadily decreasing harvest, degraded oyster grounds, and a diminished industry. It is not clear if the brood stock of the Bay has been depleted to the point that recruitment has been influenced negatively, but it may be significant that spat settlement has been poor during recent years when salinities have been low enough to inhibit disease organisms yet high enough to allow for normal reproduction. Many oyster beds are in danger of being smothered by sediments because they have been scraped so much that they barely project above the surrounding soft sediment. Silt-covered shells are not attractive to settling larvae.

Diseases

Mid-Atlantic Bight populations of oysters are subject to the diseases known as "MSX," "SSO," and "dermo".^{3,32,92} Except for the more marine SSO which does not occur in the Chesapeake Bay, these diseases have heavily depleted Bay oyster populations over the past 40 years. In addition to causing mortality, MSX inhibits growth and gametogenesis in spring. However, temperature-associated remission of infection may occur in summer and allow for gametogenesis and spawning to proceed.³¹ Similar results have been obtained for Louisiana populations infected by dermo.⁶² Of the two diseases, MSX is inhibited by salinity; salinities below about 10-15 ppt and above 30-32 ppt are associated with decreased parasite activity of MSX.³⁵ Dermo seems to be more tolerant of low salinity^{61,75} than MSX. One of the most pressing problems facing resource managers is that of understanding and combating these two disease organisms.

Contaminants

Overview

An extensive and hard-to-manage literature exists on toxicants, pollutants, pesticides, etc. It cannot readily be condensed for easy comprehension. Contaminants affecting oysters in Chesapeake Bay include heavy metals, pesticides, PCB, PAH, chlorine-produced oxidants, and petroleum hydrocarbons.^{6,36} Selected information has been compiled previously,^{42,44,66} and a comparative toxicology of marine organisms is available.^{77,81} Information on biological effects and body burdens of selected pollutants in the eastern oyster is summarized in Tables 2, 3 and 4.

It is difficult to generalize about the oyster's sensitivity, either to classes of contaminants, or relative to other species. However, adult and juvenile oysters appear to be somewhat more tolerant of most environmental toxicants than embryos and larvae, and more tolerant than some other estuarine species.

Judging from the diverse and inconsistent body of studies summarized in the Tables, the substances of most concern for toxicity to adult oysters in chronic exposures appear to be tributyltin (TBT), a few heavy metals, and petroleum hydrocarbons. Chlorinated pesticides and PCB (Arochlor 1016) caused acute mortality or sublethal effects in juvenile oysters at relatively low concentrations ($\sim 10 \mu\text{g/L}^{-1}$). Embryos were quite sensitive to mercury and silver, showed moderate sensitivity to copper and zinc, and were relatively insensitive to other metals and most of the pesticides tested. For the few substances tested, larval sensitivities were similar to those of embryos.

Interpretation of toxicity tests

Reisch⁸⁰ reviewed the use of laboratory tests for marine organisms. Acute toxicity tests typically measure the concentrations of a particular contaminant at which 50% of the test subjects die over a given period of time, usually 48 or 96 hours. This concentration is the LC_{50} for the substance. Chronic toxicity tests measure the effect(s) of sublethal concentration on one or more attributes, such as survival, growth rate, or developmental abnormalities. Problems in the standardization of these tests often limit their comparative value. Also, laboratory studies do not simulate field conditions very well, so that a contaminant's actual effect is likely to be different from what the bioassay predicts. However, short-term toxicity tests can be a valuable diagnostic tool for ranking toxicants.⁸⁰

Heavy metals and trace elements

The physiological aspects of heavy metal contamination in oysters have been summarized in the literature.^{20,29} Empirical data indicate wide variability in the toxicity of different metals to *C. virginica* embryos (Table 2). The relative toxicity of several metals is: mercury = silver > copper > zinc > nickel > lead > cadmium > arsenic >

chromium > manganese. Similar comparisons for larval or attached life stages cannot be made due to lack of data, except that mercury, silver, copper, and cadmium show acute toxicity to adults or larvae at relatively low concentrations. Comparisons between life stages reveal that embryos tend to be more susceptible than larvae for those metals which were tested on both life stages. Comparison between embryos or larvae and attached stages is not possible because acute assays were used for embryos and larvae whereas chronic tests were used for attached oysters.

Body burdens of heavy metals for oysters collected from Chesapeake Bay (Table 3) suggest that some metals (e.g., zinc) are accumulated out of proportion to their environmental concentrations. A few additional references are available for metal contamination in oysters from the Bay.^{7,27,36}

Pesticides

Kerr and Vass⁴⁶ summarized information on the accumulation of pesticide residues in aquatic invertebrates; a comprehensive treatment of the general toxicology of pesticides was given by Matsumura.⁶⁵ Differences in biological effects and toxicological endpoints measured preclude effective comparison of the relative toxicity of different pesticides (Table 2). However, acute toxicity data suggest that *C. virginica* is less sensitive to herbicides than to insecticides. An extensive list of acute toxicity of pesticides on various life stages of oysters can be found in Table 4.

Polychlorinated biphenyls (PCB) and polynuclear aromatic hydrocarbons (PAH)

Information is available on contamination of oysters and other shellfish in limited areas of Chesapeake Bay by the environmentally very persistent and ubiquitous PCB and PAH, which are both toxic and mutagenic.^{5,6,28,36,78} (Table 3). Several PCB, along with other selected contaminants are monitored in oyster tissue at a few sites in the Bay by the National Oceanic and Atmospheric Administration's National Status and Trends Program; generally, shellfish body burdens in Chesapeake Bay tend to be lower than in several other contaminated U.S. estuaries.²⁵

Chlorine and chlorine-produced oxidants

These compounds (CPO) are produced by reactions of chlorine used for disinfection of water supplies and wastewater effluents with various compounds in the source water. Growth and mortality of adult oysters, chronic effects on spat, and larval responses have been measured at various concentrations of CPO.^{82,84,86} High mortality of juvenile oysters was observed in chronic exposures to a fairly low concentration of sodium hypochlorite (Table 2).

Petroleum

Petroleum hydrocarbons, especially the more refined products and contaminated waste oils, are very toxic to at least some bivalves (see HARD CLAM, this volume). Low concentrations of petroleum were lethal to adult oysters in chronic exposures, and to larvae in acute tests (Table 2). Additional information on oil pollution in marine environments and the effects of oil on estuarine organisms, including oysters, is available in the literature.^{1,49}

RECOMMENDATIONS

The eastern oyster is a highly resilient species that appears to be reasonably protected in Maryland by laws governing thermal discharge, effluent dechlorination, use of tributyltin, and dredging. It may be at risk in areas near industrial pollution, and laws establishing limits of pollution discharge in relation to oysters may be needed. Petroleum spills, chronic discharges of petroleum wastes, and diffuse low level loadings of some very toxic heavy metals (e.g., mercury) are possible, but undocumented threats to oysters, either locally or generally in Chesapeake Bay. But because it is not mobile for most of its life, the oyster's metabolic activity is such that regulations protecting more active species (e.g., blue crabs and striped bass) for the most part will protect the oyster. Perhaps the most pressing concerns involve improving our understanding of key aspects of the species' life history, especially disease, rehabilitating depleted oyster grounds, the basing of oyster management on scientific insight rather than on political pressure, and encouraging aquaculture.

Research

In their extensive review of the biology of the eastern oyster, Kennedy and Breisch⁴⁴ posed dozens of questions on biology and management that needed answers. Unfortunately, most of these questions remain unanswered, and it is difficult to manage what is not well understood. Particularly needed is a more thorough understanding of five major areas of oyster biology, namely larval biology, feeding and nutrition of all life history stages, genetics, disease, and the effects of pollutants. It is important that studies of disease and of genetics be pursued in order to counter the incidence of MSX and dermo in the Bay, especially if oyster farming is to be encouraged.

Improved management and rehabilitation of the oyster fishery requires thorough study of three components of oyster habitat. Here are some of the questions that need to be answered in each area:

Brood stock

What is the abundance of natural brood stock now available in different areas of the Bay? Has brood stock declined as a result of mortality due to recent disease epizootics? Is there an optimal brood stock concentration that ensures adequate spawning and is population age

distribution a factor in determining this optimal concentration, i.e., does one age group contribute more gametes than another age group?

Seed and cultch supply

How much cultch is now available in the Bay, and how much is optimal? What are the best concentrations on different bottom types or in different locations? Can any area of the Bay with a favorable current system and flushing rate be made into a good seed area, given suitable firm bottom and adequate cultch for settlement?

Growing and setting areas

The best areas still available for settlement and growth need to be determined and protected from loss of cultch and from pollution. It is not clear why some areas are historically conducive to setting (are they "larvae traps"?), but are not suitable for rapid growth and fattening, and vice versa, but the reasons must be clearly understood in order to utilize different areas effectively.

Management

As noted earlier, overfishing (and now disease) has reduced oyster populations to such a level that there are no more reefs. Rather, small mounds or relatively thin layers of shell are scattered over Bay bottom, with unproductive beds often becoming silted over. The supply of seed oysters is a limiting and critical factor in rehabilitation and management. Those areas of the Bay consistently producing adequate quantities of seed should be protected and expanded. A private oyster farming industry would encourage growth of a seed industry, as it has elsewhere in North America. Fresh shell should not be exported or used for anything other than as cultch for replenishment of the bottom because fossil shell used in Maryland's repletion program is a finite resource.

The present practice in Maryland of prohibiting dredging near oyster beds during the summer larval period helps protect oysters from excessive turbidity, as does the effort to prevent sediment from running off cleared land. Bag-less dredging or the use of special boards towed just above the bottom can help to remove sediment from depleted oyster beds in the Bay. These techniques can reduce the potential for smothering spat and can clear substrate for settlement in summer.

Oyster beds must be re-established in formerly productive locations by building up a base of firm substrate into the water column, and covering that base with oyster shell and broodstock. Recent incidences of anoxia and severe hypoxia mean that attempts should not be made to rehabilitate oyster beds in deep water (below about 10 m), but rather should concentrate in the shallows where low dissolved oxygen is relatively rare or short-lived. Also, off-bottom culture should be undertaken.

Because these immense tasks will have to be supplemented by private enterprise rather than being left to public agencies, oyster farming should be encouraged. Aquaculture will enable the private sector to distribute the tasks of cleaning, shelling, and harvesting the beds among numerous individuals and entities, rather than leaving those tasks to public agencies and a heavily subsidized industry.

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Table 1. Habitat requirements for eastern oyster eggs, larvae, spat, and adults. The critical life period is the larval period (June-August). Many ranges are broad estimates, even those based on laboratory-derived determinations, and may vary with geographic location.

Life stage	Life zone	Temperature ^a °C	Salinity ^a ppt	Sediment ^b g/L ⁻¹	pH	Dissolved oxygen mg/L ⁻¹
Eggs	water column	19-32	12.5-35 ^c 7.5-22.5 ^d	<0.25	6.75-8.75	?
Larvae	water column	19-32	12.5-27.0 ^c	<0.5	6.75-8.75	e
Spat	hard substrate (benthos)	0-32+	15.0-22.5 ^f	?	?	g
Young (30-50 mm)	benthos					< 0 at 10°C ^h 0.8-1.49 at 20°C ^h 2.75-4.98 at 30°C ^h
Adults	benthos					
survival		0-32+	0-36+	?	?	~1 (5 days)
feeding		6-32; (15-25 "optimum")	5+	<0.4	?	?
growth		6-32; (15-25 "optimum")	12+	?	?	?
gametogenesis		10+	7.5-30+	?	?	?
spawning		20±	10+	?	6-10	?

^aSalinity can affect temperature tolerances, and vice versa. Tolerance to temperature is roughly adult = spat > veliger larvae > zygotes.

^bEffects depend upon type and size of particle; experimental values have been higher than values normally encountered in nature except during intense storms.

^cAdults acclimated to 26.0-27.9 ppt; optimal egg development at 22.5 ppt and optimal larval growth at 17.5 ppt.

^dAdults acclimated to 9 ppt; optimal egg development at 10-15 ppt.

^eMedian mortality times in anoxia: 11 hours for 82 µm larvae; larval swimming rates unaffected at 0.5 mg/L⁻¹ for up to 12 hours.

^fSpat had been set at near marine salinities.

^gMedian mortality times in anoxia: 150 hours for 16 mm spat.

^hLC₅₀-PD₂ (mg/L⁻¹) causing 50% mortality after 28 days of exposure at 10, 20, and 30°C, with oysters held at 10 ppt, 20 ppt, and 30 ppt at each temperature.

Table 2. Toxicity of selected compounds to the eastern oyster. Life stages: E = embryos; L = larvae; J = juveniles; A = adults. Flow conditions: S = static; F = flow-through. Effect: M = percent mortality; G = percent reduction in shell growth.

Compound	Life stage	Temperature °C	Salinity ppt	Flow	Duration	Effect	Concentration mgL ⁻¹	Strength of effect %	Reference
METAL SALTS									
cadmium chloride	E	26	25	S	48 h	LC ₅₀	3.80		11
	A	20	31	F	20 wk	M	0.10	84	89
chromium chloride	E	26	25		48 h	LC ₅₀	10.3		11
	A	20	31	F	20 wk	M	0.10	14	89
cupric chloride	E	26	25	S	48 h	LC ₅₀	0.103		11
	L	25	24	S	48 h	LC ₅₀	0.046		14
	A	20	31	F	20 wk	M	0.050	15	89
lead nitrate	E	26	25	S	48 h	LC ₅₀	2.45		11
manganese chloride	E	26	25	S	48 h	LC ₅₀	16.0		11
mercuric chloride	E	26	25	S	48 h	LC ₅₀	0.006		11
	L	25	24	S	48 h	LC ₅₀	0.012		14
	A	25-35		F	74 d	M	0.001	<10	47
nickel chloride	E	26	25	S	48 h	LC ₅₀	1.18		11
	L	25	24	S	48 h	LC ₅₀	1.21		14
silver nitrate	E	26	25	S	48 h	LC ₅₀	0.006		11
	L	25	24	S	48 h	LC ₅₀	0.028		14
sodium arsenate	E	26	25	S	48 h	LC ₅₀	7.50		11
zinc chloride	E	26	25	S	48 h	LC ₅₀	0.31		11
	E	25	26	S	48 h	M	0.200	12.2	60
PESTICIDES									
atrazine	L	20	16	S	48 h	LC ₅₀	>30		98
abate	A	21	20-30	S	99 d	M	10	0	96
chlordane	J			F	24 h	G	0.01	35-100 ^a	10
cypermethrin	J				96 h	EC ₅₀	0.370		41
dibrom	A	21	20-30	S	99 d	M	0	96	
dieldrin	E	24	30	S	48 h	LC ₅₀	0.64		24
	J	17	31	F		G	?	50 ^a	76
endrin	E	24	30	S	48 h	LC ₅₀	0.79		24
	A	23	16	S	109 h	M	0.05	50	64
2,4-D	E	24	30	S	48 h	LC ₅₀	8.00		24
heptachlor	J			F	24 h	G	0.01	35-100 ^a	10
kepone	L				96 h	LC ₅₀	0.066		34
Kepone	J				96 h	LC ₅₀	0.012		9
toxaphene	A	28	23	F	96 h	EC ₅₀	0.016		83
TBT (tributyl tin)	A	25-28	35	F	30 d	M	0.0025	50	38
PCBs									
aro chlor 1016	J	30	29			LC ₅₀	0.010		34
CHLORINE (CPOs)									
sodium hypochlorite	J	21-33	22-35	F	12 wk	M	0.25	66	86
PETROLEUM									
Nigerian crude oil	A	25 (avg.)	21 (avg.)	F	14 wk	M	0.50	45	63
	L	22.5	21	S	48h	LC ₅₀	1.7		90
No. 2 fuel oil	A	13-25	21 (avg.)	F	8 wk	M	0.50	85	63

^aReduction in shell growth.

Table 3. Representative residues (body burdens) of selected contaminants in eastern oysters. All residues are on a wet tissue weight basis. ND = no data.

Substance	Mean Residue	Range	Remarks
TRACE ELEMENTS (mg kg ⁻¹)			
<i>means of 6 sites in Chesapeake Bay⁸⁷</i>			
aluminum	31.4	16.1-53.1	
arsenic	10.6	6.5-16.7	
cadmium	4.62	1.8-10.4	
chromium	0.3	0.1-0.9	
copper	137	31.8-340	
iron	194	170-224	
lead	0.28	0.17-0.34	
mercury	5.5	0.01-15.1	
manganese	8.3	6.8-9.1	3 sites
nickel	4.0	1.6-6.6	
selenium	2.9	1.8-3.8	
silver	2.9	0.4-6.9	
tin	0.11	0.02-0.26	
zinc	3513	1120-5480	
PESTICIDES ⁴⁶ (µg kg ⁻¹)			
DDT (total)	60	<30-710	median, 2.5 y, 6 states
	15	<10-30	mean, 2 sites, Canada
	51	ND-150	representative estimate, 8 sites, Texas
aldrin	3	ND-30	mean, 10 samples
	<10	<10-30	median, 2.5 y, 6 states
BHC-lindane	4	ND-10	representative estimate, 10 samples
	10	<10-500	median, 2.5 y, 6 states
campechlor	80	<10-1000	median, 2.5 y, 6 states
chlordan	<10	<10-10	median, 2.5 y, 6 states
dieldrin	4	ND-10	representative estimate, 10 samples
	10	<10-30	median, 2.5 y, 6 states
endrin	5	ND-20	median, 1 y, 2 sites
heptachlor	1	ND-<10	representative estimate, 10 samples
	<10	ND	median, 2.5 y, 6 states
heptachlor epoxide	<10	ND	median, 2.5 y, 6 states
methoxychlor	<10	ND	median, 2.5 y, 6 states
PAH (mg kg ⁻¹)			
Elizabeth River, Va. ⁵			
total PAH	60 (max.)	15-50	17 km transect
PCB (mg kg ⁻¹)			
Maryland shellfish survey, 1979 ²⁸			
PCB 1254	0.02 (mean)	0-0.07	

Table 4. Acute toxicity (EC₅₀) of pesticides and other chemicals to the eastern oyster.⁶⁶ Flow: S = static; F = flow-through. Life stage: E = embryos; L = larvae; J = juvenile; A = adult. Measured concentrations are indicated by *. All other concentrations are nominal.

Compound	Use	Life stage	Temperature °C	Salinity ppt	Duration h	Flow	Concentration µg/L ⁻¹	95% Confidence Interval
acephate	insecticide	E	25	20	48	S	150000	800-300000
acrolein	herbicide	J	21	30	96	F	55	
acrylamide	polymer	L	20	20	48	S	>100000	
aldicarb	insecticide	E	25	20	48	S	8800	1400-56000
aldrin	insecticide	J	30	27	96	F	15	
aminocarb	insecticide	J	27	27	96	F	>1000	
amobam	fungicide	J	23	26	96	F	>1000	
anilazine	fungicide	J	10	24	96	F	40	
antimycin A	piscicide	J	26	28	96	F	62	
arochlor 1016	industrial (PCB)	A	28	28	96	F	10	
arsenic trioxide	rodenticide	J	15	22	96	F	>1000	
aspon	insecticide	J	23	28	48	F	32	
atrazine	herbicide	J	28	28	96	F	>1000	
azinphos-methyl	insecticide	J	29	28	96	F	>1000	
bensulide	herbicide	A	24	15	96	F	450	
benzene								
hexachloride	insecticide	J	27	27	96	F	190	
bromacil	herbicide	J	23	25	96	F	>1000	
bromopropylate	acaricide	J	14	30	96	F	150	
butylbenzyl phthalate	industrial	L	20	20	48	S	780	560-1000
cacodylic acid	herbicide	J	19	28	90	F	>1000	
calcium arsenate	insecticide, herbicide	J	13	31	96	F	>1000	
captafol	fungicide	J	20	26	96	F	34	
carbaryl	insecticide	J	29	27	96	F	>2000	
carbofuran	insecticide, nematocide, miticide	J	30	29	96	F	>1000	
carbophenothion	insecticide, acaricide	E	20	20	48	S	99	96-102
chlordane	insecticide	J	29	27	96	F	10	
chlordecone	insecticide	A	20	21	48	S	66	60-74
chlorobenzilate	acaricide	J	28	25	96	F	180	
chloropropylate	acaricide	J	19	26	96	F	280	
chlorothalonil	fungicide	J	29	27	96	F	26	
chlorpyrifos	insecticide	E	25	20	48	S	2000	1500-2800
clonitralide	molluscicide	J	11	22	96	F	>1000	
coumaphos	insecticide	J	9	21	96	F	290	
		J	30	23	96	F	880	
creosote	wood preservative	A	21	21	96	F	710	410-1000
crotoxyphos	insecticide	J	10	28	96	F	1000	
		J	28	28	96	F	>1000	
2,4-D butoxy-ethanol ester	herbicide	J	18	29	96	F	2600	
		A	18	29	96	F	3800	
2,4-D isooctyl ester/EPTC	herbicide	A	29	25	96	F	1000	
2,4-D propylene glycol ether ester	herbicide	A	28	25	96	F	55	
dalapon sodium salt	herbicide	J	31	28	96	F	>1000	
DCPA	herbicide	J	27	30	96	F	620	
DDD	insecticide	J	20	30	96	F	25	
DDE	DDT residue	J	12	25	96	F	14	
DDT	insecticide	J	30	23	96	F	9	

EASTERN OYSTER

Compound	Use	Life stage	Temperature °C	Salinity ppt	Duration h	Flow	Concentration µg/L ⁻¹	95% Confidence Interval
DEF	herbicide	E	25	20	48	S	700	
		J	10	27	96	F	100	
		J	27	27	96	F	200	
demeton	insecticide,							
	acaricide	J	24	13	96	F	>2000	
diamidfos	nematicide	J	19	22	96	F	>1000	
diazinon	insecticide,							
	nematicide	J	25	28	96	F	>1000	
dicamba	herbicide	J	28	28	86	F	>1000	
dichlobenil	herbicide	J	24	24	96	F	2500	
dichlofluanid	fungicide	J	29	25	96	F	35	
dichlorvos	insecticide	J	30	25	96	F	>1000	
dicofoi	acaricide	J	24	25	96	F	21	
dicrotophos	insecticide	J	29	28	96	F	>1000	
dieldrin	insecticide	J	22	25	96	F	15	
		A	17	31	96	f	31*	6-62
diquat	herbicide	J	20	29	96	F	720	
dithianon	fungicide	J	28	32	96	F	9.0	
diuron	herbicide	J	22	25	96	F	1800	
DMSA	herbicide	J	15	29	96	F	>1000	
endosulfan	insecticide	L	20	20	48	S	460	
endothall								
aquathol plus	herbicide	J	26	28	96	F	>1000	
endrin	insecticide	J	24	22	96	F	33	
		J	12	21	96	F	400	
		A	22	29	96	F	14*	4.0-50
EPN	acaricide,							
	insecticide	E	25	20	48	S	2200	
		J	21	29	96	F	130	
EPTC	herbicide	J	29	29	96	F	>5000	
ethion	insecticide,							
	acaricide	J	10	29	96	F	46	
		J	30	23	96	F	40	
ethoprop	nematicide	E	25	20	48	S	16000	7000-38000
ethylan	insecticide	J	16	28	48	F	120	
fenac sodium salt	herbicide	J	13	23	96	F	>1000	
		J	29	29	96	F	>1000	
fenamiphos	nematicide	J	11	29	96	F	>1000	
fenitrothion	insecticide	J	27	29	96	F	450	
fenthion	insecticide	J	22	16	96	F	360	
		J	15	23	96	F	340	
fenuron	herbicide	J	22	26	96	F	>2000	
fenvalerate	insecticide	E	20	20	48	S	>1000	
ferbam	fungicide	J	25	27	96	F	52	
fonofos	insecticide	J	25	20	96	F	330	
heptachlor								
technical 74%	insecticide	J	12	21	96	F	21	
		J	29	23	96	F	17	
heptachlor								
technical 89%	insecticide	A	31	36	96	F	1.5*	
hexachloro-	fungicide,							
benzene	industrial	L	20	20	48	S	>1000	
isobenzan	insecticide	J	18	33	96	F	32	
landrin	insecticide	J	26	30	96	F	>1000	
lethane 384	insecticide	J	26	30	96	F	760	
lindane	insecticide	J	30	25	96	F	240	
malathion	insecticide	J	30	24	96	F	>1000	
		J	16	14	96	F	>1000	

Compound	Use	Life stage	Temperature °C	Salinity ppt	Duration h	Flow	Concentration µg/L ⁻¹	95% Confidence Interval
maneb	fungicide	J	13	16	96	F	>1000	
metam-sodium	fungicide, nematicide	J	15	30	96	F	>1000	
methidathion	insecticide,	J	13	22	96	F	>1000	
	acaricide	J	29	25	96	F	>1000	
methiocarb	insecticide	J	23	28	96	F	>1000	
methoxychlor	insecticide	J	19	21	96	F	90	
methyl parathion	insecticide	E	25	20	48	S	12000	1000-160000
		J	24	29	96	F	>800	
methyl trithion	insecticide, acaricide	J	30	25	96	F	140	
mevinphos	insecticide, acaricide	J	22	30	96	F	>1000	
mexacarbate	insecticide, acaricide	J	24	26	96	F	>1000	
mirex	insecticide	J	25	17	96	F	>2000	
molinate	herbicide	J	24	28	86	F	>1000	
monuron	herbicide	J	22	25	96	F	2000	
naled	insecticide, acaricide	J	30	27	96	F	590	
neburon	herbicide	J	21	28	96	F	280	
niacide-Z	fungicide	J	21	28	96	F	280	
nitrapyrin	nitrification inhibitor	J	10	29	96	F	280	
paraquat L	herbicide	J	20	26	96	F	>1000	
parathion	insecticide	J	24	31	96	F	>1000	
pentachloro- phenol	wood preservative, defoliant, molluscicide	L	20	20	48	S	>180	
pentachloro- phenol sodium salt		E	25	17	96	S	40	36-44
permethrin	insecticide	A	8	20	96	F	76*	37-120
phenol	disinfectant, industrial	E	25	20	48	S	>1000	
		J	20	30	96	F	>2000	
phorate	insecticide	E	25	20	48	S	900	
phosmet	insecticide	J	30	27	96	F	>1000	
phosphamidon	insecticide	J	25	25	96	F	>1000	
phoxim	insecticide	J	30	29	96	F	320	
prometrin	herbicide	J	27	31	96	F	>1000	
propoxur	insecticide	J	25	27	96	F	>1000	
Ronnel	insecticide	J	24	24	96	F	270	
rotenone	insecticide, piscicide	J	30	29	96	F	220	
silver nitrate	industrial	L	20	20	48	S	3.3	2.4-5.4
sodium lauryl sulfate	detergent	E	20	25	48	S	1700	1600-2000
sulphenone	acaricide	J	18	20	96	F	1200	
2,4,5-T	herbicide	J	16	20	96	F	>2000	
2,4,5-T propylene glycol butyl ether ester	herbicide	A	13	25	96	F	140	
TCA sodium salt	herbicide	J	13	23	96	F	>1000	
temephos	insecticide	J	24	27	96	F	220	
temephos EC	insecticide	J	14	26	96	F	320	
		J	26	29	96	F	170	
terbutryn	herbicide	J	14	29	96	F	>1000	
terpene poly- chlorinates	insecticide	J	25	29	96	F	35	
tetravinchlorphos	insecticide	J	17	24	96	F	>1000	
tetradifon	acaricide	J	27	27	96	F	310	
tetrasul	acaricide	J	22	25	96	F	94	
thanite	insecticide	J	11	25	96	F	25	

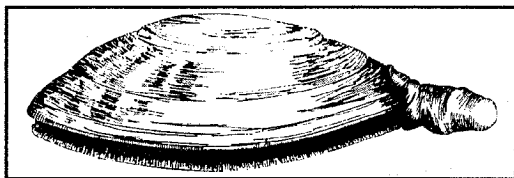
EASTERN OYSTER

Compound	Use	Life stage	Temperature °C	Salinity ppt	Duration h	Flow	Concentration μgL^{-1}	95% Confidence Interval
toxaphene	insecticide	J	31	24	96	F	34	
		A	28	23	96	F	16*	
trichlorofon	insecticide	J	30	22	96	F	>1000	
trichloronate	insecticide	J	28	28	96	F	46	
triphenyltin	fungicide	J	29	28	96	F	1.5*	
hydroxide		J	16	28	96	F	2.4	
vernolate	herbicide	J	29	28	96	F	>1000	
ziram	fungicide	J	15	22	96	F	1000	
zytron	insecticide	J	27	24	96	F	330	

SOFT SHELL CLAM

Mya arenaria

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tions persist intertidally.

Large populations of soft shell clams persist only in relatively shallow, sandy, mesohaline portions of the Chesapeake Bay. These areas are mostly in Maryland, but also occur in the Rappahannock River, Virginia. In some other portions of the Bay, especially polyhaline portions, low populations of soft shell clams persist subtidally. Restricted popula-

Soft shell clams grow rapidly in the Chesapeake Bay, reaching commercial size in two years or less. They reproduce twice per year, in spring and fall, but probably only fall spawnings are important in maintaining population levels. Major recruitment events do not occur in most years, despite heavy annual sets. Soft shell clams are important food for many predators. Major predators on juveniles include blue crabs, mud crabs, flatworms, mummichogs, and spot. Major predators on adults include blue crabs, eels, and cownose rays. Some other species that may depend heavily on soft shell clams include ducks, geese, swans, muskrats, and raccoons.

Diseases may play an important role in regulating adult populations of soft shell clams; hydrocarbon pollution is linked to increased frequency of disease. Oil pollution does the most widespread and persistent damage to soft shell clams through toxicity, aside from its role in inducing disease. Heavy metals, pesticides, and similar pollutants can be extremely toxic, but the harmful effects to clams do not last if the pollution abates. The main concern with the latter toxicants is bioaccumulation by soft shell clams, with the potential for passing toxic contaminants on to predators or to humans.

Siltation caused by storm events, dredging operations, or erosion, can smother clam populations. Eutrophication, enhanced by nutrient inputs from sewage or agriculture, is not known to have affected soft shell clam populations.

INTRODUCTION

Population levels of harvestable soft shell clams have declined since exploitation began in 1953, the first year of major harvesting of Maryland soft shell clam stocks. Harvests climbed to 3,700,000 kg in 1964 and remained stable until 1971. Harvests in Virginia began in 1955, reached a peak of 180,000 kg in 1966, but ceased in 1968. Tropical storm Agnes in 1972 was responsible for poor harvests in Maryland in the early 1970's,¹⁵⁴ but stocks had apparently collapsed in Virginia prior to the storm. In 1973 harvests in Maryland were only 300,000 kg, but rebounded to

1,400,000 kg in 1988. There has been no significant harvest of soft shell clams in Virginia since 1968.

Soft shell clams are major components of the filter feeding benthic infauna of the mesohaline portion of the Bay, consuming microscopic algae which they filter from water drawn into their incurrent siphons. There is evidence that soft shell clams are very important in removing particles from the water, even as small juveniles. A density of 3000 juveniles averaging 2.5 mm long in an area of 1 m² can filter one 1 m³ of water per day, while 1500 juveniles 5 mm long in the same area can filter 2.5 m³ per day.

Filtering capability increases exponentially with shell length.

The abundance of soft shell clams in the Bay underscores their importance as members of the benthic infauna, yet their variability in abundance (with resulting impact on the commercial fishery) suggests a role as indicator species of temporal and spatial change in the Bay environment. Below is a brief introduction to the biology of the soft shell clam, followed by a discussion of the species' habitat requirements.

BACKGROUND

Geographical Range

The soft shell clam also is known as the steamer clam or the mannose. It is found in marine and estuarine waters, intertidally and subtidally to depths of nearly 200 m along the Atlantic coast of North America from northern Labrador to Florida, with maximum abundances from Maine to Virginia.^{95,165} It also is found throughout Europe from northern Norway to the Black Sea^{60,95} and has been successfully introduced to the west coast of North America from southern Alaska to southern California.⁵⁴

Identification Aids

The soft shell clam rarely exceeds 11 cm in shell length in Chesapeake Bay,⁴ and is elongate and oval in outline. The shells gape at both ends when closed, and in life the foot and the siphons protrude from either end. The fused siphons, or "neck", are covered with a leathery integument. The shell is relatively brittle (hence the name "soft shell clam"), and in life is at least partially covered with a thin grey or tan parchment-like periostracum, whereas dead shells quickly become bleached chalk-white. Inside the left-hand shell there is a spoon-like chondrophore attached to the hinge.

Distribution, Population Status, and Trends

The distribution of soft shell clams in Chesapeake Bay is restricted by several variables, particularly salinity, sediment type, anoxia, and predation. Low salinity limits the upstream distribution in most of the major tributaries: Hog Island in the James River; Tappahannock in the Rappahannock River; Mathias Point in the Potomac River, and the Patapsco River in the mainstem Bay. Sediment type does not affect survival directly, but predators virtually eradicate soft shell clams of all sizes in soft mud, so only sandy areas contain significant amounts of clams.¹³⁵ Soft sediments predominate in deeper water; water depth therefore correlates imperfectly with soft shell clam distribution.

Seasonal anoxia is normally restricted to deep waters,^{89,164} which do not support soft shell clam populations, but periodic "seiching" events, or tilting of the density

gradient, can temporarily inundate shallower areas with anoxic water.¹⁷⁰ There is no physiological reason why soft shell clams cannot survive in deep water, and individuals have been collected in Chesapeake Bay from as deep as 15 m.¹²⁷ But populations persist mainly in shallow areas of the Bay, particularly in areas of less than 5 m. The reported persistence in shallow water may be a sampling artifact, since most sampling for adults has been done in less than 5 m;^{69,135} however, the distribution of soft shell clams is consistent with the general distribution of coarse sediments.

Although soft shell clams survive well in high salinity, indirect factors limit sustained high population levels to mesohaline portions of Chesapeake Bay. High salinity allows many predators to be active for more of the year. In shallow and mesohaline portions of the Bay, clams have more time to grow to a size that limits predation. Predation pressure therefore places an effective upper salinity limit on soft shell clam distribution.

In Chesapeake Bay optimal areas for soft shell clams are found on the Eastern Shore from Pocomoke Sound to Eastern Bay, and on the western side from the Rappahannock River to the Severn River in Maryland. The northward "deflection" of this distribution on the Eastern Shore may be due to higher salinities on that side of the Bay. Ideal conditions may exist in small areas in other portions of the Bay also, and low population densities exist throughout most of the Bay. We have chosen the relatively arbitrary level of one adult soft shell clam per m² as a definition of high abundance; throughout most of Chesapeake Bay abundance is much lower. Juvenile abundance may greatly exceed 1 m⁻² temporarily in almost any part of the Bay. Potential distribution, averaged for a variety of conditions, is shown in the Map Appendix.

Multi-year trends in salinity, temperature and anoxia may temporarily expand or contract this range. Within-year variations allow juveniles to settle in outlying areas, but these populations rarely survive more than a year.^{33,147} Juveniles often set in high abundances in areas with low adult abundance, but are virtually eradicated within months.^{69,76,77,176} In addition, episodic events such as high summer temperatures, high predator abundances, or low salinity can eradicate adults in small areas¹²⁶ or large areas.^{31,71} These areas can be recolonized quickly when conditions once again become favorable,⁶⁵ but since bi-valve larvae tend to be retained within their native subestuaries,^{105,149} severely affected subestuaries would probably take longer to recover.

Although soft shell clams reproduce twice in most years, juveniles that recruit in spring rarely survive because of predation pressure, regardless of the magnitude of recruitment.^{77,176} Only clams spawned in the fall, and therefore able to grow in cold water when predators are inactive,

survive to a size large enough to avoid most predators.¹⁷¹ Even then major recruitment events may occur only every ten to fifteen years.⁷⁰ Based upon our observations, severe temperature shifts can eliminate large numbers of recent recruits to intertidal populations in a short period. There is evidence that large amounts of drifting macroalgae can inhibit settlement of soft shell clams.¹²⁵ Attached macrophytes (c.g., submerged aquatic vegetation) on the other hand, enhance settlement by slowing currents.⁸¹ Recruitment events within different subestuaries are likely to be independent because bivalve larvae tend to be retained within subestuaries.^{105,149}

In lower regions of Chesapeake Bay soft shell clam populations are less abundant, except in intertidal areas. The intertidal region may have greater than 20 adults m⁻² while subtidal areas have virtually no adults¹⁰² (our observations). This distribution probably is due to the coarse intertidal sediments and the limited time that clams are exposed to predators.^{111,145} If spawning success is affected by the density of adults,¹²⁸ these intertidal populations are probably vital to maintaining recruitment of juveniles subtidally.

Population levels of harvestable soft shell clams have declined since exploitation began in 1953,^{173,174} but the reasons are unclear. In 1950 the hydraulic escalator harvester was invented, and in 1953 major harvesting of Maryland soft shell clam stocks began. Prior to 1953 the maximum harvest had been 730 kg (meat) in 1949,¹⁰⁸ but harvests rapidly climbed to a maximum of 3,700,000 kg in 1964, and remained nearly stable until 1971.^{173,174} Harvests in Virginia began in 1955 and were much more irregular, reaching a peak of 180,000 kg in 1966, but ceasing in 1968. Extreme mortality of adult soft shell clams in parts of Chesapeake Bay caused by tropical storm Agnes in 1972 was responsible for poor harvests in Maryland in the early 1970's,¹⁵⁴ but stocks had apparently collapsed in Virginia prior to the storm. In 1973 harvests in Maryland were only 300,000 kg, but rebounded to 1,400,000 kg in 1988. There has been no significant harvest of soft shell clams in Virginia since 1968. All evidence in Virginia (which has limited soft clam populations in most areas) suggests that large settlements of juveniles can be produced by small populations of adults.^{32,33,34,35,69} Soft shell clams also appear to be resistant to domestic sewage and low levels of industrial pollution.^{3,78,99} So little is known about fisheries dynamics that we cannot say that there are not natural population trends on the scale of decades.¹⁴⁴ Since virtually every exploited fishery stock for which data has been kept has shown a significant overall decline,¹⁴⁴ the possibility exists that declines in soft shell clam populations in Chesapeake Bay may be partially due to exploitation.

LIFE HISTORY

Spawning and Fecundity

Soft shell clams usually spawn twice per year in Chesapeake Bay; once in mid- to late autumn, and once in late spring. The actual times depend on the temperature of the water, because the clams can spawn only in water between 10-20°C, and spawn most efficiently at 12-15°C.^{102,133} Optimal temperatures occur only for a few weeks each year, and if the length of time that these conditions exist is too short, the clams may not spawn at all. This situation happens most often in spring.^{102,150,151}

During spawning both eggs and sperm are released externally. It has been found that the success rate of external fertilization for other benthic invertebrates decreases sharply with both sperm dilution and sperm age. Both of these factors increased with the distance between spawning adults, so higher densities of adults led to higher fertilization success.¹²⁸ Assuming that this principle holds true for soft shell clams, it means that areas with high adult population density contribute disproportionately to the production of larvae.

Sexes are separate in soft shell clams, with equal numbers of males and females,^{17,102} although Appeldoorn⁵ found a slight but significant bias towards females in Long Island Sound. Fecundity, or the number of eggs produced per female, increases exponentially with female size.¹⁷ A clam with a shell 3 cm long can produce only about 1,300 eggs per spawning episode, whereas a 5 cm clam can produce 9,300 eggs, and a 10 cm clam, 85,100 eggs. Larger clams, therefore, are disproportionately important in maintaining population levels.

Eggs and Larval Development

Egg size varies from about 42 to 73 µm in diameter.^{17,101} An egg develops into a trochophore larva within a day, and becomes a veliger larva in several more days. The veliger metamorphoses into a juvenile clam at about 200-300 µm in shell length^{101,119} in about one to three weeks, depending partly on temperature.^{102,163} During their larval phase bivalve larvae are planktonic, swimming just strongly enough to maintain themselves at some level of the water column. When the larvae are ready to metamorphose they alternately swim near the bottom and crawl on the bottom for several hours before settling.¹⁰¹ Gregarious settlement has been reported.⁷³ The newly settled clams, or spat, usually attach themselves to any available substrate with byssal threads secreted by the foot.¹⁰¹

Juveniles, Growth, and Adults

Although adult soft shell clams are completely sedentary, small juveniles up to about 15 mm long can be very active. If hard substrate, such as shell, worm tubes, eelgrass, or coarse sand is available, they will attach themselves to it with byssal threads. These threads are often released

while the young clam crawls about with its foot. It also may burrow temporarily during this period of its development.^{101,157} Eventually the clam burrows permanently, and unless disturbed, spends the rest of its life in place. Clams can be disturbed and redistributed by strong tidal or storm events. The depth of the burrow increases with age, so that the top of the shell can be 2 cm below the surface when shell length is only 1 cm, 4 cm deep at a size of 2 cm, and 12 cm deep at 4 cm.¹⁸⁷

Growth of soft shell clams in Chesapeake Bay is relatively rapid. Under average conditions, they can reach the marketable size of 5 cm (shell length) in 1.5-2 years.^{64,107} Growth rate depends on many factors, including salinity and temperature, food abundance, sediment type, intertidal level, and pollution. Both high salinity and warm water, especially in spring, favor growth.^{4,110,162} Food abundance - measured both by actual abundance and by competition with other filter-feeders - affects growth.¹⁶²

Fine sediments favor growth, whereas sand and gravel decrease growth rates.¹²³ (This does not mean that mud is better soft shell clam habitat, however, as explained below in the **Habitat Requirements** section.) Intertidal clams grow more slowly both because they have less time to feed, and because the sediment tends to be coarser.⁸² Some types of pollution have been shown to decrease clam growth rates, as explained under **Special Problems** below. Growth is best in summer and poorest in late winter,¹²¹ and most growth is completed within the first five years of life. Growth decreases exponentially with age, but clams 28 years old have been found.^{18,103} There is no evidence that genetic differences between populations or subpopulations affect growth rate.¹⁵⁹

ECOLOGICAL ROLE

Role as Filter Feeder

Soft shell clams feed on microscopic algae which they filter from water drawn into their incurrent siphon. They consume small flagellated cells and diatoms in the 5-50 μm range,^{43,110,153} and can selectively reject non-food particles and toxic dinoflagellates such as *Protogonyaulax tamarensis*.^{43,152} Rejected particles are incorporated into pseudofeces, and thus are removed from the water column. Free-living bacteria are too small to be filtered,¹⁸⁴ but bacteria associated with detritus may be assimilated.⁹² The presence of soft shell clams affects the settlement of many species of infauna, enhancing some and inhibiting others. Although rarely, some invertebrate larvae are drawn into the siphons,⁵¹ the mechanisms of interactions between soft shell clams and infaunal settlement are not known. Differential filtration may be a contributing factor.⁷⁵

Studies of soft shell clams outside of Chesapeake Bay suggested that the clams were very important in removing

particles from the water, even as small juveniles. In San Francisco Bay, it was calculated that a density of 3000 juveniles averaging 2.5 mm long in an area of one m^2 could filter one m^3 of water per day, while 1500 juveniles 5 mm long in the same area could filter 2.5 m^3 per day. The filtering capability of adults was not calculated, but it increased exponentially with shell length.¹²⁴ These densities are high for Chesapeake Bay,¹⁰² but even much lower densities may be significant. In waters off western Sweden, it was estimated that infaunal bivalves, including high numbers of soft shell clams, consumed nine times as much of the small plankton as did zooplankton grazers.¹⁰⁰ Filtering by benthic filter feeders is especially important in controlling microalgal biomass associated with eutrophication in shallow, well-mixed bodies of water, such as Chesapeake Bay.

When compared to other common Chesapeake Bay filter feeders, soft shell clams equal or exceed eastern oysters in weight-specific filtering rates, but filtering rates are lower than those of jackknife or razor clams. Ribbed mussels can filter bacteria from the water, whereas soft shell clams cannot.^{88,153}

Role of Empty Shells

Despite its fragility, the shell of the soft shell clam is relatively resistant to dissolution, and its light weight makes it less likely to be buried than many shells.⁴² Thus, the shell is particularly suitable as substrate for many fouling organisms, especially in areas that lack other shell or rock. Most of these fouling species are small, but two bivalve species make extensive use, directly or indirectly, of soft shell clam shells. The jingle shell requires a smooth, hard surface (such as soft shell clam shells) as a substrate, and the ark clam settles onto hydroids that grow on the shells.⁴¹

Predators

Predation on soft shell clams at all stages is very intense. Under most conditions 90% to over 99% of fertilized eggs and planktonic larvae are destroyed in the water column.^{166,185} Jellyfish (hydromedusae and scyphozoans) and comb jellies are considered major predators of molluscan larvae.^{129,139} Sea nettles, although abundant for part of the year, normally are not present when soft shell clam larvae are abundant.¹⁷⁹ Other potential predators on mollusk larvae include copepods, larval and juvenile fish, and filter-feeding fish such as anchovies and menhaden.^{27,129,139,146} As the larvae metamorphose and settle, they fall prey to benthic planktivores such as barnacles, sea anemones, and annelid worms.^{15,160,186} Mortality of newly-settled juveniles is about 90% within the first several days.¹³⁸

It is thought that overall predation is the most important source of mortality for all juvenile and adult age classes. Benthic planktivores in high abundance can prevent set-

tlement locally.¹⁸⁶ Predators can eradicate soft shell clams from an area, whether newly-settled juveniles,^{50,69,80,138} or older juveniles.^{76,77,119,176} Predation can keep populations from surviving in muddy substrates, where it is easier to dig down to the clam.⁹⁷ Although larger clams are less vulnerable to predation, a high abundance of predators can destroy a local clam population.¹²⁶

Soft shell clams provide an important, direct link between phytoplankton and predators of all sizes. The relative importance of a predator on juvenile or adult clams depends both upon the proportion of its diet that is made up by soft shell clams and its overall abundance. For most predators one or both of these factors is not known, so their importance can only be estimated. Table 1 lists major and minor predators on juvenile soft shell clams, and Table 2 lists major and minor predators on adult clams. "Major" predators are defined here as animals that are abundant throughout most of the soft shell clam range in Chesapeake Bay and use soft shell clams as a significant portion of their diet. "Minor" predators are those that are not abundant, are restricted to a small proportion of the Bay, or for which soft shell clams are only a minor portion of the diet. "Juveniles" are here defined as clams with shell lengths of under 2 cm.

Mummichogs are limited to very shallow water,⁷⁴ but the other major predators are found in all water depths that sustain large soft shell clam distributions. Their importance as clam predators relative to each other is not known. Submerged aquatic vegetation reduces predation on infaunal bivalves.¹³⁰ Polychaete worms certainly have the capability of preying on juvenile clams;^{53,96} Hidu and Newell⁷³ reviewed evidence suggesting that some polychaete worms are major predators.

Of the minor predators, horseshoe crabs, snapping shrimp, and oyster drills are abundant mainly in polyhaline areas. Mud snails are abundant in Chesapeake Bay, but less so in sandy areas, and apparently eat only extremely small bivalves.⁸⁰ Ducks and geese affect only shallow areas, but are active in winter, when most other predators are inactive.^{61,83}

Adult soft shell clams, if they can be excavated, are vulnerable to predators because their shells are fragile and do not close tightly. The method of predation by eels is unknown, but crabs can excavate to 20 cm or more (personal communication: R. Lipcius, Virginia Institute of Marine Science), and rays can, by means not well understood, excavate large pits to reach adult clams (personal communication: R. Blaylock, Virginia Institute of Marine Science). Of the minor predators, all but the black drum are limited to polyhaline portions of the Chesapeake Bay.

Many species of predators, especially fish, eat mainly siphon tips of soft shell clams.^{74,180} These injuries usually

are not lethal to clams, but reduce the fitness of individuals, so the effects at the population level are approximately equal to the effects of removing an equal biomass of entire individuals.

Some populations of certain other species may depend heavily on soft shell clams, even though they are not numerically important predators. These predators include ducks and geese, especially overwintering populations,^{61,83} and muskrats and raccoons (personal communication: J. Carlton, Oregon Institute of Marine Biology).¹⁶⁷

There are four ways soft shell clams can escape most predation pressure. The first is to grow larger, because larger clams are buried deeper, and deeper clams are harder for predators to excavate.^{11,76,176,187} The second is to live in coarser sediments (e.g., sand rather than mud) where predators have more difficulty excavating.⁹⁷ It follows, therefore, that even though clams grow faster in soft mud,¹²² large populations cannot persist in mud in Chesapeake Bay.¹³⁵ The third partial refuge is low temperature. Clams can survive and grow at low temperatures,^{12,66} when their predators are inactive. Consequently, they grow to a larger, less vulnerable size before their predators become active.¹⁷¹ The fourth partial refuge is intertidal areas, an exception to the general distribution of soft clams. Intertidal areas are limited in extent in most parts of Chesapeake Bay, but soft shell clams are well-adapted to intertidal existence.² Intertidal areas provide a relative refuge from most predators, because there is less time for predation;^{111,145} areas that do not support significant subtidal populations can sometimes support intertidal populations of adults.^{69,102} Some predators, such as mummichogs, ducks, geese, whistling swans, and raccoons, are well-adapted to this zone, however, so the intertidal area is only a partial refuge. Recreational clam harvesting also occurs mainly in the intertidal region.

Low density is also thought to be a partial refuge from predation, because predators tend to seek out patches of high density prey.⁹⁷ The value of this tactic to the soft shell clam, however, probably is offset by the lower success rate of fertilization among low-density clam populations, as hypothesized above under **Life History**.

HABITAT REQUIREMENTS

Water Quality Salinity

According to Matthiesen,¹¹⁰ adults cannot survive below 4 ppt salinity for more than a few days, and do not grow below 8 ppt, but Chanley²⁵ reported survival after acclimatization at 2.5 ppt. Probably the lower summer salinity limit is 8 ppt. Larval salinity tolerance varies, depending upon the salinity to which the adults are acclimated,¹⁶³ but Chanley and Andrews²⁶ give 5 ppt as a lower limit. There is no upper salinity limit, but the prevalence of predators

in water of high salinity restricts large populations of soft shell clams in the Bay to mesohaline areas. Adults can survive salinities as low as 0 ppt for about two days,¹¹⁰ but longer periods cause mass mortalities.⁷⁰ Juveniles are more susceptible to low salinity than adults, and warm temperature decreases tolerance to low salinity.

Temperature

Soft shell clams can survive temperatures as low as -12 °C for long periods of time¹², so normally there is no lower temperature limit in Chesapeake Bay. Sudden and extreme temperature shifts may affect intertidal populations of juveniles, however, although Kennedy and Mihursky⁸⁷ reported that juveniles are more tolerant of temperature extremes. A sudden decrease in air temperature from 20°C to below 0°C in a few hours was followed by massive mortalities of intertidal juveniles within a day in the York River (our observations). Only juveniles recruited the previous autumn were affected. Because such temperature shifts occur mainly in the winter, they represent a major source of mortality for clams during a time when most predators are inactive. Only intertidal populations are likely to be affected, however.

Optimum temperatures for feeding are about 16-20 °C, but feeding can take place at as low as 1.5°C,⁶⁶ a temperature much lower than the minimum required for activity by most soft shell clam predators. The upper limit for soft shell clams is about 34°C,⁶⁶ a temperature rarely encountered in Chesapeake Bay. Temperature extremes do limit spawning, however, since spawning is restricted to temperatures between 10-20°C at the most.¹⁰² Optimal spawning probably is restricted to an even narrower temperature range.¹³³ These temperatures are required for a period of at least several weeks for gamete maturation and successful spawning. In some years, especially in spring, temperatures rise or fall too quickly for successful spawning.^{102,151} Larvae evidently can grow at a wide range of temperatures, and growth rate is independent of temperature within certain limits.¹⁰²

pH

Seawater is naturally buffered in the salinity ranges occupied by soft shell clams, so extreme pH is unlikely to occur. Consequently there has been little study of the effects on soft shell clams of pH variations. Physiological processes in soft shell clams occur without significant inhibition over a relatively wide range of pH.¹⁶¹

Dissolved Oxygen and Depth

Although soft shell clams can survive near-anoxic conditions for as long as seven days,¹¹² anoxia has been known to cause mass mortalities of soft shell clams in western Sweden.¹⁴³ Seasonal anoxia in some deep portions of the Chesapeake Bay^{89,164} has minimal impact on soft shell clam populations because they are restricted largely to shallow areas. If anoxia is extensive, however, and pro-

longed "seiching" events, or tilting of the density gradient, occur, anoxic deep water can inundate shallow areas¹⁷⁰ and cause mortalities of benthic organisms. It is not known to what extent anoxia in the Bay is enhanced by domestic sewage and agricultural runoff, but these inputs correlate with anoxia and mass soft shell clam mortalities in waters off western Sweden.¹⁴³ If eutrophication and the extent of seasonal anoxia in the Chesapeake Bay are increasing, as some have suggested, the frequency and duration of shallow water anoxic events also will increase. A "catastrophic" anoxic event in 1984 apparently threatened shellfish beds in Maryland.¹⁴⁸

Structural Habitat

Adult soft shell clams removed from their burrows eventually die unless they can reburrow;⁷² they can reburrow quickly only into very soft sediments.¹³⁶ Although they grow most quickly in soft sediments,¹²³ they are also most vulnerable to predators there.⁹⁷ Large populations in Chesapeake Bay persist only in muddy sand and sandy mud.¹³⁵ Soft shell clams can survive in very coarse sediments (our observations).¹²²

SPECIAL PROBLEMS

Contaminants

Metals

Industrial pollution typically contains a suite of metal ions in various concentrations, termed "heavy metals." Soft shell clams sampled from areas with heavy-metal pollution grow significantly more slowly than clams in unpolluted areas,³ and are in generally poor condition,⁵⁷ but recovery is rapid when heavy-metal pollution ceases.³ Table 3 lists some of these metals and their measured toxicities. Compared to other aquatic organisms, soft shell clams are particularly vulnerable to copper and mercury. Copper is bioaccumulated slightly more in low salinity than in full seawater,¹⁸³ so soft shell clams in Chesapeake Bay are particularly vulnerable.

Tributyltin (TBT), until recently a component of most marine antifouling paints (its use on large vessels continues), is believed to be extremely toxic to most marine organisms, and is bioaccumulated at high rates by filter feeders such as soft shell clams.⁹³ The toxicity of organotins to soft shell clams has not been studied.

Metallic aluminum particles are apparently nontoxic to soft shell clams.⁶³

Pesticides, Chlorine, Polychlorinated Biphenyls

A variety of pesticides, including DDT, endrin, dieldrin, and endosulfan have been shown to be toxic to soft shell clams, but recovery is rapid when exposure ends.¹⁴¹ Chlorine-produced oxidants, a byproduct of sewage treatment, in concentrations as low as 0.3 mgL⁻¹ kill 50% of soft shell clam larvae with only 16 hours of exposure.¹⁴²

Polychlorinated biphenyls (PCB), formerly used in many industrial products, have been suggested as causes of poor condition in soft shell clams from polluted areas.⁵⁷ Even in highly polluted areas, however, such as the Elizabeth River in Virginia, low populations of adult soft shell clams persist.¹⁴⁰

Petroleum and Petroleum Products

Petroleum, both crude and refined, and its by-products, including polycyclic aromatic hydrocarbons (PAH), are toxic to soft shell clams. Oil spills can be particularly damaging. In muddy sand, such as that found in Chesapeake Bay, spilled oil penetrates slowly but remains for years, and destroys increasingly larger clams over time, eventually eliminating most of the population.⁴⁰ Clams transplanted to oil spill areas also die out due to the oil.³⁹ Depending on the dose and the type of oil, the growth rates of survivors are significantly reduced. Bunker C and Number 6 fuel oil have been shown to reduce growth by as much as 50% in survivors.^{3,58,59,104} Hydrocarbons extracted from polluted sediments are more than ten times as toxic to soft shell clams as they are to fish.¹⁶⁸ Not all oil pollution has been shown to have adverse effects,¹ but crude oil is bioaccumulated by soft shell clams.⁵⁵

The role of hydrocarbon pollution in diseases of soft shell clams has been debated, but in general high incidences of cancer-like diseases correlate with hydrocarbon pollution. Neoplasia, hyperplasia, and germinoma have all been correlated to hydrocarbon pollution of various types.^{7,67,177} Brown *et al.*²⁰ did not find a correlation with total hydrocarbon pollution, but did find a correlation between neoplasia and total PAH levels. Polynuclear aromatic hydrocarbons have been implicated as carcinogens, and are common components of hydrocarbon pollution. This is an example of an indirect effect of human impact, and there are others which probably go unnoticed.

Bioaccumulation

From a human viewpoint, the most serious aspect of pollution in a fishery species is bioaccumulation. Many pollutants are bioaccumulated, or concentrated, by soft shell clams, some of which are thought or known to be extremely toxic to humans. An indirect danger is that sublethal quantities of toxicants will be accumulated further by predators of soft shell clams, such as blue crabs, which are also fishery species.

Two studies on soft shell clam bioaccumulation of heavy metals and organochlorine residues in Maryland^{46,47} showed no dangerous levels, but all compounds examined were bioaccumulated to some extent. Soft shell clams bioaccumulated most of the toxicants less than or equally to oysters, but arsenic, which was increasing in sediments, was bioaccumulated more than by oysters. Mercury and cadmium were not bioaccumulated in high

amounts, probably because of their toxicity to soft shell clams. However, blue crabs, which feed on soft shell clams, showed greater accumulation of these metals.

Tributyltin is accumulated by soft shell clams far more than by non-filter feeders, and over 50 times more than by sediments.⁹³ A pesticide (diquat) however, was present in lower amounts in soft shell clams than in sediment.⁶⁸ Chrysene, DDT, and naphthalene were not bioaccumulated from sediments; diethyl ether and dioctyl phthalate were accumulated from sediments only in trace amounts,⁵⁶ but this did not mean that they were not bioaccumulated from the water. Butler²³ found that soft shell clams accumulate all pesticides tested (aldrin, DDT, dieldrin, endrin, heptachlor, lindane, and methoxychlor) to a greater extent than hard clams but also decreased their body burdens better than hard clams when exposure stopped. Both crude oil and PAHs are bioaccumulated by soft shell clams, even when levels in the water are very low.^{58,118} Copper and zinc, on the other hand, are accumulated far less than by oysters.¹¹⁴

Diseases

Soft shell clams in the Mid-Atlantic Bight area are subject to a variety of cancer-like diseases, which may be directly due to a viral agent.³⁰ The agents of these diseases are not known, and there are no standard descriptions of most of them, but at least four cancer-like diseases have been described. These include: neoplastic proliferation of tissue (usually mantle) that invades other tissues; hematocytic neoplasia, or leukemia,¹⁵⁸ an extreme increase in the number of hemolymph cells; hyperplasia, or proliferation of gill tissue; and germinoma, or proliferation of gonadal tissue.^{67,177}

Only one of these diseases, described as an epizootic sarcoma, and probably synonymous with neoplasia, has been studied in Chesapeake Bay. It was implicated in mass mortalities in parts of the Maryland Eastern Shore, where up to 65% prevalence was found in sampled populations, with 100% mortality of diseased clams.⁵² Hematocytic proliferation, however, has been found with up to 40% incidence in Rhode Island, with 50% mortality of diseased clams.²⁹

Other diseases include hypoplasia, or defective gonadal development, and lipofuscin deposits, or brown pigmented areas.¹⁷⁷ No mortalities have been reported for hypoplasia, but if the incidence is high, a significant proportion of the population effectively could be castrated. Lipofuscin deposits are not known to be pathogenic, but are more prevalent in polluted areas.²¹ The role of pollution in many of the above diseases, especially neoplasia, is fairly well established. Although pollution may not cause these diseases, certain forms of pollution are well-correlated with incidence of neoplasia^{7,20,21,67,177} as discussed below.

A series of soft shell clam mass mortalities in 1970 and 1971 in Maryland led to an investigation of pathogenic bacteria, and eight pathogenic bacteria were discovered. Whether any of these caused the mortalities is not known, but it demonstrated that bacterial diseases may be important ecological factors in soft shell clam populations.⁸⁵ The role of disease in regulating soft shell clam populations has not been studied widely, but existing information suggests that diseases of all sorts may be as important as environmental factors or predators in adult clam population dynamics.

The most alarming soft shell clam pathogen from a human viewpoint is paralytic shellfish poisoning, caused by the planktonic dinoflagellate *Alexandrium (Gonyaulax) tamarensis*. This species is apparently toxic to soft shell clams, which reduce feeding and reject the dinoflagellates when they are present. For this reason, up to ten days after the start of a bloom there is no significant accumulation of the algal toxins by soft shell clams.¹⁵² Fortunately, *A. tamarensis* does not bloom frequently in Chesapeake Bay. Paralytic shellfish poisoning therefore is not considered a problem in this location.

Although parasites probably are present, they have not been studied in soft shell clams in Chesapeake Bay. Probably the most serious parasite is the cercaria stage of the trematode *Himasthia leptosoma*, which replaces muscle tissue in clams (mud snails and various shore birds are hosts for the parasite's other life stages). A number of other trematode species have been identified in soft shell clams in New England and Canada.²⁸ A turbellarian flatworm has been found in soft shell clams, but apparently it is not clear whether it is parasitic. The commensal nemertean *Macrobdella grossa* probably is not parasitic. A ciliate protozoan has been identified as a parasite, but does not appear to be common.²⁸ Two copepods have been identified as occasional parasites in soft shell clams. The parasitic pea crab is strictly polyhaline,¹⁸² as are the ectoparasitic snails,¹⁷⁹ so they do not affect most soft shell clams in Chesapeake Bay.

Sewage and Eutrophication

Soft shell clam populations can persist in areas with high domestic pollution,⁷⁸ but a high organic content, characteristic of sewage-polluted sediments, correlates with reduced growth rate of soft shell clams.¹²⁰ One effect of sewage, however, is eutrophication, which can enhance regional anoxia.

So far eutrophication has not been a problem for Chesapeake Bay soft shell clam populations. Evidence from Sweden indicates that domestic sewage can enhance eutrophication catastrophically, leading to widespread anoxia with total eradication of infauna (including soft shell clams), so the danger probably exists in Chesapeake Bay.

Disturbance

Heavy siltation can occur from dredging operations or storms. Survival of adult soft shell clams buried by sediments varies with the kind of sediments. Burial by up to 24 cm of coarse, mud-free sand can be survived, but only 6 cm of fine sand and only 3 cm of silt can be fatal.¹⁶⁹ New channels occasionally are dredged in shallow areas, e.g., for creation of marinas, with obvious direct effects on any clams in the path of the channel. But most often existing channels, which do not support significant clam populations, are deepened or widened. If the dredged material is very fine, much of it may drift over adjacent areas and bury soft shell clams, which are susceptible especially to burial by fine sediment.

Hydraulic escalators, used to harvest soft shell clams in Chesapeake Bay, do relatively little damage to surviving clams. Incidental mortality of unharvested clams is about 7%, incidental catch of fish and crabs is largely nonlethal, and oysters more than 30 m away are unaffected.^{106,115,134} This compares to about 50% mortality of unharvested clams by hand methods used in New England.¹¹⁶ Delicate burrow systems and submerged aquatic vegetation are totally eradicated by the hydraulic harvesters, however.¹⁰⁶ The use of the hydraulic dredge has been reviewed by Kyte and Chew.⁹⁰

Intertidal populations of soft shell clams are the only significant pool of adults in some parts of Chesapeake Bay,^{69,102} so destruction of intertidal areas by shoreline construction, erosion, landslides, or other factors can have a disproportionately large effect on soft shell clam populations. Conversely, landslides can help create habitat for soft shell clams in the intertidal and shallow subtidal regions of the Bay if they replace unsuitable sediment with suitable sediment. The effects of shoreline destruction, as well as bottom disturbance, by wakes and propeller wash from the increasing number of recreational boats, has not been studied in this context, but at this point effects are probably minor and local.

Power Plants

"Extensive" mortalities of soft shell clams were reported in the Patuxent River in Maryland after the Chalk Point power plant was constructed, presumably due to heated effluent.¹¹⁷ Studies specifically designed to study the effect of heated water near Calvert Cliffs, Maryland, however, failed to show any harmful effects to soft shell clams.^{76,77,99} This is a complex issue, in part because spawning, which is temperature-related, may also be affected by heated effluent.

CONCLUSIONS AND RECOMMENDATIONS

Harvesting

The fertilization and settlement patterns of soft shell clams described above suggest that as long as each subestuary

has reserved a small but sustained pool of adult soft shell clams, and as long as care is taken not to destroy newly settled clams by disturbance or sedimentation, harvesting will have no long term population effects. Since denser populations probably have better spawning success, for optimum effect the reserve population of adults in each subestuary should be in an area that traditionally sustains high densities of adults. Since domestic sewage apparently has no serious direct effects on soft shell clams, one possibility is to use areas condemned for shellfish harvesting because of domestic sewage as adult reserve areas.

Although hydraulic escalators used to harvest soft shell clams in Chesapeake Bay do relatively little damage to unharvested soft shell clams or incidental catches of mobile fauna, submerged aquatic vegetation and oyster reefs are destroyed completely. The preservation of submerged aquatic vegetation and oyster reefs, because of their importance in the ecology of Chesapeake Bay, should in all cases take precedence over soft shell clam harvesting;

however, harvesting can occur within about 100 m of these communities with little harm.

Pollution

Because copper is the most deadly heavy metal to soft shell clams, any pollution monitoring in areas where soft shell clams are a concern should include measurements of copper ion concentrations.

Because oil spills lead to massive clam mortalities and, in areas with sublethal pollution, cause reduced growth rates, measures to protect the Bay from oil spills are important to preserving soft shell clam habitat.

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SOFT SHELL CLAM

Table 1. Predators on juvenile soft shell clams in the Chesapeake Bay.

Major Predators	Minor Predators
Polychaete worm (<i>Nereis virens</i>) ^{73,96}	Flatworm (<i>Stylochus ellipticus</i>) ⁹¹
Blue crab (<i>Callinectes sapidus</i>) ^{97,176}	Polychaete worms (Eunicidae, Nephtyidae Nereidae) ^{53,96}
Mud crabs (Xanthidae) ^{65,69,104,181}	Mud snails (<i>Ilyanassa obsoleta</i> , <i>Nassarius</i> spp.) ^{69,80}
Shrimp (<i>Crangon septemspinosa</i>) ^{6,137}	Moon snail (<i>Polinices duplicatus</i>) ⁴⁴
Mummichogs (<i>Fundulus</i> spp.) ^{74,86}	Oyster drills (<i>Urosalpinx cinerea</i> , <i>Eupleura caudata</i>) ²⁴
Spot (<i>Leiostomus xanthurus</i>) ^{74,76,77}	Horseshoe crab (<i>Limulus polyphemus</i>) ^{13,14}
	Amphipods (Gammaridae) ⁵⁰
	Snapping shrimp (<i>Alpheus</i> spp.) ⁸
	Hermit crabs (<i>Pagurus</i> spp.) ⁶
	Croaker (<i>Micropogonias undulatus</i>) ⁷⁴
	Winter flounder (<i>Pseudopleuronectes americanus</i>) ^{6,94}
	Tautog (<i>Tautoga onitis</i>) ¹⁰
	Ducks (<i>Anas</i> spp., <i>Aythya</i> spp.) ^{61,83}

Table 2. Predators on adult soft shell clams in the Chesapeake Bay.

Major Predators	Minor Predators
Blue crab (<i>Callinectes sapidus</i>) ^{97,176}	Ribbon worm (<i>Cerebratulus lacteus</i>) ⁸⁴
Eel (<i>Anguilla rostrata</i>) ¹⁸⁰	Moon snail (<i>Polinices duplicatus</i>) ^{45,79}
Cownose ray (<i>Rhinoptera bonasus</i>) ^{126,155,156}	Whelks (<i>Busycon</i> spp.) ³⁸
	Skates (<i>Raja</i> spp.) ^{74,155}
	Rays (<i>Dasyatis</i> spp.) ⁷⁴
	Black drum (<i>Pogonias cromis</i>) ⁷⁴

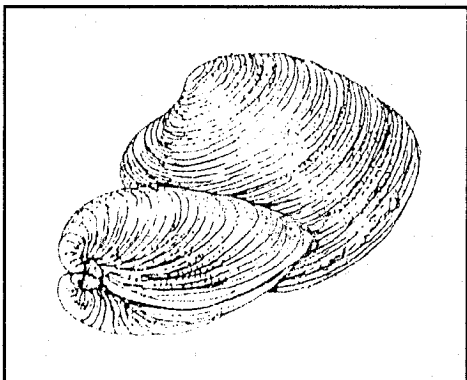
Table 3. Toxicity of metals to soft shell clams: LC₅₀ is the concentration that is lethal to 50% of the sample in a 7 day time period. Data from Eisler⁴⁸ and Eisler and Hennekey.⁴⁹

Metal	LC ₅₀ (mgL ⁻¹)	Metal	LC ₅₀ (mgL ⁻¹)
Cadmium (Cd ²⁺)	0.15-0.7	Manganese (Mn ²⁺)	300
Chromium (Cr ⁺⁶)	8.0	Mercury (Hg ²⁺)	0.004
Copper (Cu ²⁺)	0.035	Nickel (Ni ²⁺)	30
Lead (Pb ²⁺)	8.8	Zinc (Zn ²⁺)	3.1

HARD CLAM

Mercenaria mercenaria

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The hard clam is found along the eastern coast of North America from the Gulf of St. Lawrence to Texas. In Chesapeake Bay, the hard clam is restricted to salinities above approximately 12 ppt. An extensive survey of hard clam resources is overdue. Statements concerning long term trends in populations are not feasible.

Hard clams grow to a maximum shell length of about 120 mm. There are few documented cases of diseases in wild hard clam populations. Parasitic infestations are also slight. The life cycle of the hard clam includes a pelagic larval phase and a relatively sedentary benthic juvenile and adult phase. In Chesapeake Bay, ripe gametes can be found between May and October, and spawning

commences when temperatures rise above 20-23 °C. The larvae are planktotrophic (feeding). Metamorphosis usually commences at a shell length of 200-210 mm. Predation on new recruits is very high; dense aggregations of hard clams have been found in the absence of predators. Aside from predation and fishing pressure, the natural mortality of larger clams appears very low.

Hard clams are important suspension-feeding infauna, thus they are important in grazing of primary production, transfer of carbon and nitrogen to benthic food chains, and, through excretion, rapid recycling of particulate nitrogen as ammonia. The major food source for hard clams is planktonic microalgae. In Chesapeake Bay, growth occurs in spring and fall, when optimum water temperatures coincide with abundant food.

Clams are capable of living in a variety of sediment types, but higher abundances are found in coarse-grained sediments. Hard clam stocks are susceptible to overfishing. Recruitment rates are poorly understood, as are possible reestablishment periods if areas are depleted through commercial harvesting, and factors influencing larval settlement rates.

Hard clam mariculture is well established and could easily be expanded into sites within the Bay.

Given the ability of clams to bioaccumulate toxic substances, adequate monitoring should be maintained. The sublethal effects of toxic material readily found in the lower James River should be examined.

INTRODUCTION

The hard clam is an important member of the suspension-feeding, benthic infauna of the lower Chesapeake Bay, where it exists in salinities above 12 ppt. Commercially exploitable stocks exist in several areas of the Virginia

portion of the Bay and have become increasingly important in recent years as watermen look for alternatives to the declining oyster fishery. In the face of continuing threats from bayside development and stock exploitation, comprehensive surveys of the hard clam in the Bay are long overdue; much data is over 20 years old. The purpose

of this document is to provide the reader with a broad summary of aspects of the natural history of the hard clam in the Chesapeake Bay so that potential impacts of shoreline development and other activities affecting the aquatic environment can be assessed in terms of environmental requirements of the hard clam in the Bay.

BACKGROUND

Geographic Range

The hard clam also is commonly known as the quahog, little-neck clam, or cherrystone clam. It is distributed along the Atlantic coast of North America from the Gulf of St. Lawrence to Florida and along the Gulf of Mexico coast from Florida through Texas.^{1,58} The hard clam has been introduced to California and Europe.^{7,70} It is restricted to salinities above approximately 12 ppt, and is most abundant in polyhaline estuarine waters. Its depth range extends from the intertidal zone to greater than 18 m.⁵⁸

In Chesapeake Bay, *M. mercenaria* is the only common hard clam. Baywide surveys of clam populations are few; however, the hard clam's potential estuarine distribution is mainly determined by salinity, and it is not abundant below 18 ppt. In the Maryland portion of the Bay, hard clam populations are restricted to Pocomoke and Tangier Sounds,⁸¹ although deposits of old shells are found in the lower Patuxent. The bulk of the Chesapeake hard clam distribution is located in the Virginia portion of the Bay, particularly in subestuary river systems with salinities exceeding about 12 ppt and depths greater than 5 m.^{6,34} Surveys have found hard clams to be widely distributed in the Chesapeake Bay, but commercially exploitable abundances are limited to an area of about 12,000 acres. These high density distributions are concentrated in the lower York and James rivers.⁶⁸ Limited commercially exploitable abundances are also found in the lower Rappahannock River, Mobjack Bay, and along the western side of the Eastern Shore.^{65,67,68}

Distribution and Population Status

The potential habitat of hard clams in Chesapeake Bay includes areas where the bottom salinity exceeds 12 ppt, which corresponds to approximately 17 ppt during summer; larval metamorphosis is impeded below 17 ppt.^{40,87} Adult hard clams can tolerate salinities to about 12 ppt, but do not grow. Hard clams are capable of small local migrations, pushing out of the sediment and moving before the current. An 18 mm clam can be moved by a 25 cm s⁻¹ current. The abundance of clams within a habitat is simply the number of larvae which settle minus those that die after settlement. The surviving clams may then be redistributed by local currents. Comprehensive studies of larval densities and settlement rates have not been made for Chesapeake Bay sites. Limited data have been reported for areas outside the Bay. Carriker³² reported a density of 572 larvae L⁻¹ in Little Egg Harbor, New Jersey,

whereas seed densities as high as 270,000 m⁻² have been recorded in Maine.⁴⁷

Because regular surveys of hard clam resources in Chesapeake Bay have not been made, long term trends in populations cannot be determined. Results of several local surveys of hard clam populations in the Virginia portion of the Chesapeake Bay are summarized in Table 1. Unexploited populations of hard clams in the Chesapeake Bay usually are composed of significantly more large individuals than new recruits or juveniles.^{68,72} In the bulk of the populations sampled by Haven *et al.*,⁶⁸ greater than 70% of the clams were more than 6 cm in shell length, with an estimated age of 4-8 years. In another survey, the highest density of clams smaller than 3.6 cm in shell height was found to be only 0.44 clams m⁻², compared with a density of 3.22 clams m⁻² for clams larger than 5.8 cm at the same site.⁷² In the James River, where densities of adults were among the highest in the Bay, the estimated annual recruitment was less than one clam m⁻².^{65,68} Low recruitment may be the result of high larval mortality, low settlement rates, heavy predation on post-settlement clams or some combination of these factors. The hard clam is a long-lived species, and individuals have been aged at more than 30 years.^{64,91}

Morphology

Hard clams grow to a maximum shell length of about 120 mm. The valves of the hard clam are thick, inequilateral, ovate-trigonal, and joined at the hinge by a thick brown external ligament. The shell is sculptured with fine concentric ridges which separate and coarsen at the umbones, while at mid-shell the ridges diminish to a characteristic smooth spot. The valves do not gape. A distinguishing external feature is the heart-shaped lunule, located anteriorly to the prominent external ligament. The lunule is typically 3/4 as wide as long. Internally, the ventral margin of the shell is crenulate. The hinge architecture is strong, and the anterior and posterior adductor muscle scars and the pallial sinus are prominent.

The outer shell of hard clams ranges in color from yellowish to white, although specimens collected from reduced sediments may be darkly colored. The interior of the shell is usually white, tinged with dark purple patches. The shells were valued by American Indians as wampum.⁵⁸ Growth patterns within the shell may reflect the environmental history of the individual.⁹⁰ The basic anatomy of hard clams conforms to that of venerid bivalves. The shell-secreting mantle lines the valves and encloses the viscera, and is fused postero-ventrally into the short inhalant (incurrent) and exhalant (excurrent) siphons. The siphons are muscular and retractable, ending in tactile and chemosensitive tentacles. The strong, hatchet-shaped foot extends antero-ventrally and is used to burrow into the substrate.¹⁰

LIFE HISTORY

Spawning and Reproduction

The life cycle of the hard clam is typical of other venerid bivalves, and includes a pelagic larval phase and a relatively sedentary benthic juvenile and adult phase.^{32,87}

The hard clam is a protandrous, consecutive hermaphrodite and is dioecious after changing sex (i.e., the clams begin adult life as males, often become females with greater maturity, and require individuals of both sexes for reproduction). Sexual maturity is mainly a function of size.^{17,84,85,104} Clams develop functional male gonads at 6-7 mm in shell length in the first or second year of life. Oocytes are sometimes present at this time. After this juvenile male phase definitive sexes are established at a size of about 30 mm shell length.^{7,54,83,84}

Spawning cycles are affected mainly by temperature and food availability, and thus vary according to latitude. From north to south, the development and duration of ripe gametes tends to begin earlier and extend longer.⁵⁴ Spawning often occurs in pulses and may continue for months,⁴⁴ but usually there are one or more distinct spawning peaks; a second spawning peak often occurs from North Carolina south.^{2,54} When ripe gametes have been produced, spawning is stimulated by a temperature increase over some threshold. In Chesapeake Bay, ripe gametes can be found between May and October,³⁷ and spawning usually commences when temperatures rise above 20-23 °C⁶ (personal communication: M. Castagna, Virginia Institute of Marine Studies).

Fecundity in hard clams is high. Females can release 16-24 million eggs per spawn,⁴⁴ although laboratory studies often have recorded lower values of 1-3 million eggs.⁷⁸ With repeated spawns individuals may release up to 60 million eggs over a season. The viability of eggs and subsequent survival of larvae are positively related to egg size, not clam size,^{7,79,88} but the amount of spawn released increases with increasing clam size.¹⁷ Eggs are 60-85 µm in diameter when released, and covered with a gelatinous membrane which expands in contact with water, further extending the diameter to 163-179 µm.³² In culture experiments, however, eggs will often pass through a 35 µm mesh; they are retained on a 25 µm mesh. Fertilization occurs in the water column.

Larval Development

The larvae of hard clams are planktotrophic (feeding), and development of the larval forms follows the usual blastula, gastrula, trochophore, straight-hinged (90-140 µm), umboed (140-220 µm), and pediveliger (170-230 µm) stages of bivalve molluscs.^{37,87} Rate of development is highly dependent on temperature, salinity, availability of high quality food, and turbidity; under optimum conditions the larval stage can be completed in as little as a week.⁸⁶ On

the other hand, the larval stage can be maintained for at least 24 days if conditions are inadequate or suitable substrate is lacking.⁸⁶

Mature pediveliger larvae have a well-developed, ciliated foot and byssus gland in addition to a functioning velum.³² The pediveligers alternate swimming with crawling on the bottom using the foot. This behavior facilitates testing the substrate for suitable settling sites. Pediveligers can distinguish between different sediment types, although the selective mechanisms involved are unclear.⁷⁶ Distribution of settling larvae within the estuary probably reflects a combination of active site selection and passive deposition.^{24,129} During settlement, the pediveliger anchors itself to the substrate with a byssal thread, thereby terminating the period of planktonic life.³² It is unclear whether the velum is absorbed or cast off at settlement. Degeneration of the velum may precede settlement. The ciliated foot of the pediveliger also serves as a swimming organ. The settled clam is now termed a "byssal plantigrade", which slowly metamorphoses into a juvenile clam. Metamorphosis is gradual, and entails development of the digestive viscera and gills, fusion of the mantle edges, and development of the siphons. Metamorphosis usually commences at a shell length of 200-210 µm.⁸⁷

Young byssal plantigrades initially lie at or just under the sediment surface, but can move about on the foot, while the byssal threads can alternately be detached and reformed. The exhalent siphon usually is developed at metamorphosis, but the inhalent siphon usually does not appear until a shell length of approximately 1.5 mm. As the siphons develop and elongate, the byssal plantigrade burrows progressively deeper in the substrate. The siphons initially maintain contact with the overlying water, but after the formation of siphonal tentacles, which aid in the exclusion of sediment from the inhalent stream, the clam may be completely buried. At a shell length of about 7-9 mm, the byssal gland is lost and the byssal plantigrade becomes a juvenile plantigrade. The juvenile clam can move about by means of the shortened, hatchet-shaped foot.³²

Growth

The hard clam exhibits seasonal, latitudinal, and size-related variations in growth.^{8,55} In warm-temperate areas such as Chesapeake Bay, the most significant growth occurs in spring and fall, when optimum water temperatures coincide with abundant food (see **Habitat Requirements**). Growth decreases in summer, and ceases in winter (at water temperatures less than 9°C). Seasonal growth increments increase along the north-south latitudinal gradient; thus clams grow to market size earlier in areas with longer growing seasons.⁸ Growth rate also tends to decrease with age.^{55,102} As growth ceases either with old age or adverse conditions, clams become thicker ("blunt") rather than increase in shell length.

Hard clams exhibit wide geographical variation in growth rates. Growth model estimates indicate that 2.5 years are needed for clams to reach 3.8-5 cm, and 4.5 years to exceed 6 cm on Hampton Flats, Virginia. In contrast, in the lower salinity areas of the York River, 4-5 and 8 years are required to reach the respective size classes. Chowder clams at the same locations were estimated to be 8-20 years old.^{65,67,82}

ECOLOGICAL ROLE

Feeding

Hard clams are important members of the suspension-feeding infauna. Therefore, they are important in benthic-pelagic coupling, grazing of primary production, transfer of carbon and nitrogen to benthic food chains, and through excretion, rapid recycling of particulate nitrogen as ammonia. The major food source for hard clams is planktonic microalgae.

Normally, clams lie buried in the substrate with only the siphons communicating with the sediment surface. Specialized gill cilia draw a respiratory and feeding current down the inhalant siphon, through the gills, and out the exhalant siphon. Food particles brought in by the inhalant stream are filtered out by cilia, trapped in mucus strings, and transported to the labial palps, where the material is sorted by size. Organic and inorganic particles in the size range of about 5-15 μm are imbedded in mucus strings and ingested. Material rejected from the sorting cilia on the gills or labial palps is concentrated near the base of the inhalant siphon and periodically ejected by forceful adduction (closing) of the valves. The rejected material is called pseudofeces. The sensory tentacles on the inhalant siphon can reduce the aperture to limit inhalation of sediment.

Filtration rates of hard clams are related to food concentration. Feeding efficiency increases with increasing particle density up to a maximum, and then decreases at higher particle concentrations.¹¹⁹ Optimum algal density for hard clam filtration is 2×10^5 cells ml^{-1} .¹¹⁸ Clams have been observed to assimilate 71.2-77.3% of the ingested food.¹¹⁹ Maximum filtration rates were found to be dependent on the species of algae.¹²⁵ Feeding rates also increased directly with temperature and current velocity.¹²⁵

Predation

Predation on newly recruited hard clams is very high, and is known to have eliminated entire sets of both natural and planted stock.^{9,33,67,93,97} Dense aggregations of hard clams were found in the absence of predators.⁹² In Chesapeake Bay, the blue crab appears to be the primary predator on juvenile hard clams,^{5,33,56,66} although oyster drills, whelks, and mud crabs also are significant predators.^{6,56} Flatworms can cause problems where clams are cultured out of their natural substrate. The cownose ray is

common in Chesapeake Bay¹⁴ and is capable of feeding on the larger sizes of hard clams.^{6,35} Other important predators include horseshoe crabs, herring gulls, and finfish (tautog, puffer, black drum, and flounder).⁵⁴ Many predator species prevalent in other areas (e.g., sea stars) are prevented from affecting Chesapeake Bay hard clam populations by low salinity.

The size of clams interacts with crab size and substrate characteristics to form refuges from predation.^{56,57,92,127} Crabs feed by crushing small clams and chipping away the edges of larger clams,¹¹⁴ but clams larger than about 6 cm shell length are immune from most crab predators.⁵⁴ Boring gastropods (e.g., oyster drill snails) also probably prey more extensively on thinner-shelled, younger individuals. Intense predation on small individuals may explain their poor representation in the size-frequency distributions of populations. Densities of clams often are higher in seagrass beds than in surrounding sand flats,¹⁰⁰ and gravel or shell aggregate has been shown to reduce crab predation.^{35,57,92}

Aside from predation and fishing pressure, the natural mortality of larger clams appears to be very low.⁶ Clams maintained in predator exclusion cages in South Carolina had an estimated mortality of 1.43%.⁴⁹ There are few documented cases of diseases in wild hard clam populations,¹¹³ although the hard clams in Canada reportedly were decimated by disease.¹¹⁶ Parasitic infestations also are slight.⁵⁴

HABITAT REQUIREMENTS

Water Quality Temperature

Temperature affects hard clam reproduction, and growth of larvae and adults. Gametogenesis begins when water temperature reaches about 10°C,⁵⁴ and temperature is one of the main stimuli for spawning. Critical spawning temperatures vary geographically due to acclimation of populations to local conditions.⁷⁸ In Chesapeake Bay, spawning usually begins in May when water temperatures rise above 23°C.^{75,77}

Younger life stages generally have narrower temperature tolerances for survival than adults. Eggs remain viable from 7.2-12.5°C to over 32.5°C,^{43,77,89} but embryos and trochophores at temperatures above 30°C experienced increased mortality with increased exposure time.⁷⁷ Larvae survived temperatures between 12.5 and 30-33°C;^{32,87} the best survival rate was between 22.5-25.0°C at 22.5 ppt salinity.⁴³ Adult hard clams can survive temperatures between -6 and 45.2°C,^{69,129} Activity of adults is curtailed below 1°C and above 34°C,^{63,123} and is optimal between 21 and 31°C.¹¹⁹

Larval growth and survival are functions of both temperature and salinity.^{73,89} Growth of larvae ceases at <12.5°C,⁸⁷

mainly because the larvae cannot assimilate ingested food.⁴³ The optimum temperature for growth at most salinities (≤ 27.0 ppt) is 25–30°C, and the optimum temperature range for larval growth from fertilization to ten days at 21.5–30 ppt salinity is 22.5–26.6°C. Temperature also affects the developmental rate of larvae: the time between fertilization and settling has been found to be 20 days at 18°C (16–24 days) and 7.5 days at 30°C (7–9 days). Growth of adults occurs between 8°C and about 31°C,^{3,12} with an optimum temperature of 20°C.^{3,102,109} The latter values are below those quoted earlier¹⁰⁹ and probably reflect inhibition of bacterial activity at the lower temperatures.

Salinity

Salinity significantly affects both growth and survival of hard clams. Larval forms are more sensitive to adverse salinity levels than adults. The salinity range for normal egg development is 20–35 ppt,^{40,43} with an optimum of about 27 ppt.⁸⁷ High mortality occurs at less than 12–17 ppt.^{34,36,87} The upper and lower salinity limits for normal larval development are 15–35 ppt, indicating that larvae can exist in lower salinity regimes more successfully than eggs.⁸⁷ Metamorphosis, however, is inhibited at less than 17 ppt.^{40,87} Optimum salinity for growth and survival to settlement is 26–27 ppt.^{34,40,43,87}

The synergistic effect of salinity and temperature on larval growth and survival results in a limiting of the ranges of temperature tolerance with a reduction in salinity, especially at high temperatures and low salinities.⁴³ Thus higher mortalities and slower growth of larvae are expected at less than 17.5 ppt. The minimum salinity tolerance for adults is approximately 12 ppt, whereas clams can exist in waters of oceanic salinity¹¹⁴ and above. For example, hard clams have been recorded in Laguna Madre, Texas, at salinities up to 48 ppt! The ability of hard clams to adduct the valves tightly reduces the negative effects of short term environmental fluctuations. Reproduction is inhibited at less than 15 ppt.³⁴ Thus salinity is a major factor in hard clam distribution patterns. In Chesapeake Bay, clams are not abundant at less than 20 ppt⁶ (personal communication: M. Castagna, Virginia Institute of Marine Science).

Dissolved Oxygen

Dissolved oxygen (DO) usually is not a limiting factor for hard clams in Chesapeake Bay. Anoxic events usually are concentrated in lower salinity, upper Bay areas outside the salinity tolerance range for metamorphosis, or in deeper regions where clams are scarce. Additionally, clams of all life stages exhibit a marked tolerance to low DO. The minimum DO requirement for normal development is about 0.5 mgL⁻¹, although growth rates are reduced greatly below 4.2 mgL⁻¹.⁹⁸ Short term stress does not affect later development.⁹⁸ Adult hard clams can maintain oxygen consumption down to DO levels of 5.0 mgL⁻¹,

after which oxygen consumption declines and, presumably, anaerobic metabolism becomes responsible for a greater proportion of total metabolic activity.^{62,63} Dissolved oxygen concentrations of less than 5.0 mgL⁻¹ clearly represent stress to hard clams. Activity can be maintained even at DO concentrations less than 1.0 mgL⁻¹.¹⁰⁹

Turbidity

Heavy sediment loads have negative effects on growth and survival, although clams usually can tolerate ambient concentrations of suspended materials. Eggs suffered increasingly abnormal development with increasing silt concentration from 0.75–3 gL⁻¹; at the higher concentration, there was no normal development.⁴¹ Larvae were not able to survive or grow in concentrations of 0.25 gL⁻¹ chalk or 0.50 gL⁻¹ of fuller's earth, although eggs could withstand higher concentrations.^{41,45} Growth of larvae was inhibited in silt concentrations above 0.75 gL⁻¹, however, survival was high even at 4 gL⁻¹.^{41,45}

High concentrations of small particles tended to clog the larval alimentary tract.⁴⁵ Juvenile and adult clams (14 and 32 mm shell length) decreased the ingestion rate of algae with increasing sediment load (up to 0.044 gL⁻¹), and lost 18% of ingested algae by increased production of pseudofeces.¹⁸ The rate of filtration also was depressed by additions of silt.¹⁰⁵ Growth of hard clams was inhibited at 0.044 gL⁻¹, but not at 0.025 gL⁻¹.¹⁹ Most of these detrimental concentrations are higher than those encountered in nature, except during dredging or very heavy runoff events.

pH

Hard clams are tolerant of most pH levels commonly encountered in their habitats. Embryos developed at pH values of 7.00–8.75, whereas larvae survived in the pH range of 6.25–8.75.^{26,27} Growth occurred between pH 6.75–8.50, with an optimum between pH 7.50 and 8.50.^{26,27}

Structural Habitat

Substrate characteristics are important for hard clam growth, distribution, and abundance. Larvae prefer to settle in sand over mud substrates, but particle size was not deemed an important factor.⁷⁶ Clams are capable of living in a variety of sediment types. Field surveys often have found higher abundances of hard clams in sandy rather than muddy sediments; however, this distribution varies by location.^{3,4,126} A heterogeneous substrate mixture of sand or mud with gravel or shell often shows high abundances of clams.^{101,117} This fact appears to relate to the larger material offering a spatial refuge from predation.⁹ Higher growth rates also have been observed in sand substrate.^{38,60,90,102}

SPECIAL PROBLEMS

Contaminants

The toxic action of a number of organic and inorganic compounds on hard clams has been investigated. The ability to culture hard clams has allowed for the evaluation of many compounds on the larval stages. Embryos and larvae are much more susceptible to toxicants than are adults. The adults often can withstand large body burdens of toxic materials, and can concentrate these substances far above ambient concentrations. Additionally, the depuration of toxic compounds is often slow. This consideration is of obvious concern because hard clam populations, especially in the James River, often are exposed to toxicants. One important aspect of pollution biology, sublethal effects (e.g., reduction of reproductive output), is poorly understood. The following section on toxicants refers to values of LC_{50} and EC_{50} , defined as follows:

LC_{50} = concentration of a toxicant that causes death of 50% of the test organisms;

EC_{50} = concentration of a toxicant that affects a specific response (e.g., growth) in 50% of the test organisms.

Organic Compounds

Concentrations of petroleum products in the low mgL^{-1} range are toxic to embryonic and larval clams (Table 2). These concentrations were measured in the field following a spill, as well as tested experimentally in an oil-spill weathering simulator.²⁵ Growth studies with EC_{50} end points indicated that petroleum products decreased growth rates when compared to controls.²⁵ This sublethal effect is important because increased mortality of clams usually is associated with longer planktonic existence. The hard clam is very sensitive to waste motor oil, which makes up a significant portion of petroleum pollution.²⁵

Hydrocarbon depuration is slow. Adult hard clams depurated only about 30% of accumulated hydrocarbons in 120 days (41.9 – $29.3\ mg\ kg^{-1}$ wet weight).¹⁶ Clams with initial benzo(a)pyrene contamination levels of $16.0\ \mu g\ kg^{-1}$ reduced body burdens to $8.2\ \mu g\ kg^{-1}$ after seven weeks and had a residual of $1.1\ \mu g\ kg^{-1}$ after 60 weeks.¹¹¹ Oiled sediments reduce the depth to which clams bury while increasing burial time.⁹⁹

Polynuclear aromatic hydrocarbons (PAH) were found to accumulate in hard clams much faster than they were depurated, giving bioaccumulation factors in the 10^3 – 10^4 range¹³ (Table 3); however, oysters were found to have even higher bioconcentration factors because they had significantly lower depuration rates than hard clams.¹³

In contrast to the relative tolerance levels of temperature and salinity on the early life stages of hard clams, the

toxicity of the insecticides, herbicides, bacteriocides, and fungicides tested usually were greater for larvae than for eggs^{42,45} (Table 4). The relative LC_{50} concentrations of the compounds vary, but generally are in the mgL^{-1} range.^{42,45} Some compounds (sevin, endothal, 2,4-D salt, phenol, and sulmet) accelerated larval growth over controls; the reasons were unclear, but antibiotic properties or chelation of toxicants were suspected. Except for allyl alcohol, the organic solvents tested were not toxic.⁴⁵ Hard clams concentrate pesticides, but do not store polychlorinated hydrocarbon pesticides as well as other species (Table 5). Accumulation of a variety of pesticides was slower and depuration was faster in hard clams than in soft shell clams.^{22,23} The biotic concentration factor (BCF) is a function of contaminant concentration. At a DDT concentration of $1.25\ gL^{-1}$, the maximum mean BCF in hard clams after 18 days was 1.8×10^3 , whereas the depuration time was slightly over three months.³⁹ Butler²¹ reported tissue accumulations of $6\ \mu g\ g^{-1}$ after one week at a DDT concentration of $1\ \mu g\ gL^{-1}$ ($BCF = 6 \times 10^3$). At higher concentrations, DDT decreased in foot tissue after six months while the concentration in the viscera did not decrease measurably.³⁹ Fortunately, DDT use now is banned in the United States.

Tributyltin oxide (TBTO) was found to be highly toxic to hard clam eggs and larvae, with LC_{50} values in the parts per trillion (ngL^{-1}) range for eggs and embryos, and the μgL^{-1} range for larvae and juveniles (Table 6).¹⁰⁶ A TBTO concentration of $0.77\ ngL^{-1}$ depressed growth rates, although the resulting larvae were normal.¹⁰⁶

Kepone contamination of the James River estuary was recognized in 1975, and the substance was found to be present throughout the food chain. Hard clams had comparatively low body burdens of the insecticide, and no directly toxic effects were discovered.⁷³

The sublethal effects of chlorinated hydrocarbon contamination include depressed glucogenesis and enhanced glucose degradation. These conditions indicate stress in the organism.⁵² Other enzyme pathways may be affected.⁵²

Hard clam embryos and larvae have been found to have relatively low tolerances to surfactants⁷¹ (Table 7). Forty-eight hour LC_{50} values ranged between 0.0085 – $5.83\ mgL^{-1}$; actual field concentrations of surfactants in the St. Mary's River, Maryland, were reported at $0.06\ mgL^{-1}$.⁷¹ Again, clam larvae were more tolerant than oyster larvae. In contrast, sodium nitrilotriacetic acid (NTA) was non-toxic to adult oysters;⁵¹ 168-hour LC_{50} values were more than $10\ mgL^{-1}$. Hard clams were the least sensitive species examined.

Inorganic Compounds

Juvenile and adult clams were relatively unaffected by high concentrations of ammonia and nitrite (Table 8); nitrate and orthophosphate had no deleterious effects⁵³. The lethal values for these compounds are higher than normally encountered. In contrast, chlorine was highly toxic to hard clam larvae, with EC₅₀ values near the $\mu\text{g L}^{-1}$ level.^{107,110}

Heavy metals were toxic to eggs and larvae of hard clams in the $\mu\text{g L}^{-1}$ to mg L^{-1} range (Table 8).^{28,29,30,31} Metals are known to be concentrated in hard clams at several orders of magnitude greater than in the surrounding environment. Accumulation and depuration rates are dependent on such physical factors as temperature and salinity which affect metabolic rates.¹⁰³ In hard clams taken from Southampton, England, metal accumulation was related inversely to salinity, but little correlation was found between sediment metal and tissue metal concentrations.¹⁰⁸ Generally, depuration rates of heavy metals from hard clams are slow. Levels of cadmium, chromium, nickel, lead, zinc, and copper either remained the same or increased after transplantation from a polluted area in Great South Bay, New York.¹¹ Accumulation rates, body burdens, and depuration rates of heavy metals in hard clams are low relative to oysters and soft clams.¹⁰³ Oxygen consumption rates increased with increasing silver concentrations.¹²⁰

Heavy metal toxicity varies with life stage and types of metal. Early life stages are more sensitive to mercury and silver than to cadmium, possibly due to a lower accumulation rate for cadmium, but the order of toxicity to these metals reverses in older animals, perhaps due to tolerance to mercury and silver.³⁰ The relative toxicity of metals to hard clams was found to be copper > cadmium > chromium > zinc,¹¹² whereas metal toxicity to hard clam larvae was determined to be mercury > copper > silver > zinc > nickel (nickel was relatively nontoxic).³¹ Body burdens of cadmium, copper, and zinc were determined in hard clams from the James and York Rivers and several sites in Chesapeake Bay.⁸⁰ The concentrations of these metals within samples (zinc 5.0-112 $\mu\text{g g}^{-1}$, copper 1.0-16.5 $\mu\text{g g}^{-1}$, and cadmium < 0.8 $\mu\text{g g}^{-1}$) generally were comparable with other studies; however, the metal content of clams in the James River was higher than in the York River or in the mainstem Bay, suggesting heavy metal contamination in the James.⁸⁰

RECOMMENDATIONS

Research

The ability to manage a resource requires a firm knowledge of the status of the resource. The abundance and distribution patterns of hard clams in Chesapeake Bay are poorly described and are based upon information from studies of nearly 20 years ago. A more extensive contem-

porary survey of hard clam resources is urgently needed. Further, the early life history of hard clams in the Bay has not been investigated. Larval settlement rates and annual recruitment, and the factors which influence these processes are poorly understood. Basic research is needed to address these problems.

Harvesting

Hard clam stocks are susceptible to overfishing. Recruitment rates are poorly understood, as are possible reestablishment periods if areas are depleted of clam populations by commercial harvesting. Hydraulic dredges are efficient harvesting tools capable of eliminating the bulk of the clams in an area. Patent tongs probably are much less efficient and allow some clams to persist under present fishing stress. Control of the method of harvest is a prudent measure to control fishing mortality.

Mariculture

Hard clam mariculture is well established and easily could be expanded into sites within Chesapeake Bay, although site specific salinity might influence clam growth and hence, the economic viability of mariculture endeavors.

Toxics

Given the ability of hard clams to bioaccumulate toxic substances, an adequate system to monitor body burdens of toxicants should be maintained. The sublethal effects on clams of toxic substances readily found in the lower James River should be examined.

CONCLUSION

The hard clam clearly is an important member of the suspension feeding infauna and contributes significantly to grazing of single-celled plankton, to coupling of benthic and pelagic food chains, and to nutrient recycling in Chesapeake Bay. The hard clam also supports a significant commercial industry. Information gaps in hard clam distribution and abundance need to be filled. The deleterious effects of anoxia, turbidity, and toxic organic and inorganic compounds on hard clams need to be monitored carefully. The hard clam is a suitable candidate species for mariculture and is unusually free of natural diseases and parasites.

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HARD CLAM

Table 1. Literature reports of hard clam densities in the Virginia portion of the Chesapeake Bay.

Site	Density clams m ⁻²	Reference	Site	Density clams m ⁻²	Reference
Hampton Bar, James River	8.7-11.1	68	Allens Island, York River	3.9	68
Poquoson Flats	2.4	68	Gaines Point, York River	6.8	68
Lower James River	0.7-4.7	72	Mobjack Bay	1.3-2.1	68

Table 2. Toxicity of petroleum products to hard clams.²⁵ All LC₅₀ and EC₅₀ values are in mgL⁻¹.

	Embryos LC ₅₀				Larvae EC ₅₀	
	48 h	96 h	144 h	240 h	144 h	240 h
Kuwait crude	12	25	13.1	2.0	15.7	4.2
Southern Louisiana crude	5.7	6.0	5.3	2.1	3.2	1.1
Bunker C	1.0	3.2	1.8	1.6	1.9	1.0
No. 2 fuel oil	0.43	1.3	1.3	0.53	0.63	0.57
Florida Jay crude	0.23	0.25	0.11	0.55	0.29	0.22
Used motor oil	0.04	0.10				

Table 3. Concentration of polynuclear aromatic hydrocarbons (PAH) by hard clams.¹³ Uptake rate: 28-day accumulation in mg kg⁻¹d⁻¹; Clearance: 28-day clearance rate in mg kg⁻¹d⁻¹; BCF: bioconcentration factor.

Compound	Uptake rate	Clearance rate	BCF
Benzo(a)anthrene	2824	0.172	16516
Benzo(a)fluorene	994	0.167	5943
Benzo(b)fluorene	1190	0.162	7332
Benzo(a)pyrene	361	0.087	4143
Benzo(e)pyrene	2366	0.148	15980
Benzo(ghi)fluoranthene	3384	0.145	23306
Benzo(a)fluoranthene	1857	0.180	10331
Chrysene	1190	0.162	7335
Fluoranthene	1477	0.213	6934
Methylphenanthrene	187	0.115	1628
Methylpyrene	2002	0.148	13571
Perylene	1133	0.161	7059
Phenanthrene	224	0.114	4072
Pyrene	1587	0.194	8172
Total PAH	556	0.137	4072

Table 4. Toxicity of pesticides to hard clam eggs and larvae.^{42,45}

Compound	Eggs: 48 h LC ₅₀ mgL ⁻¹	Larvae: 12 day LC ₅₀ mgL ⁻¹
Insecticides		
aldrin	>10	0.41
co-ral	9.12	5.21
dicapthon	3.34	5.74
di-syston	5.28	1.39
guthion	0.86	0.86
lindane	>10	>10
N-3514	<1	<1
sevin	3.82	2.50
toxaphene	1.12	<0.25
Herbicides		
diuron	2.53	>5
endothal	51.02	12.50
fenuron	>10	>5
monuron	>5	>5
neburon	<2.4	<2.4
Nematocide		
Nemagon	10	0.78
Solvents		
acetone	>100	>100
allyl alcohol	1.03	<0.25
orthodichlorobenzene	>100	>100
trichlorobenzene	>10	>10
Bacteriocides, Algicides, Fungicides, etc.		
chloramphenicol	74.29	50
Delrad		0.072
Dowicide A	>10	0.75
Dowicide G	<0.25	<0.25
griseofulvin	<0.25	<1
PVP-Iodine	17.10	34.94
Nabam	<0.50	1.75
nitrofurazone	>100	>100
phenol	52.63	55.00
Omazene	0.081	0.378
Phygon	0.014	1.75
Roccal	0.19	0.14
Sulmet, tinted	>100	>100
Sulmet, untinted	>1000	>1000
TCC	0.032	0.037

Table 5. Accumulation and depuration of pesticides by hard clams.

Compound	Life stage	Dose $\mu\text{g L}^{-1}$	Accumulation mg kg^{-1} tissue	Depuration mg kg^{-1} tissue	Reference
DDT	Adult	1	3-9	3.5 (0 d) 0.88 (10 d) 0.161 (20 d)	20
		1 (7 d) 0.0125 (18 d)	6 10.0 \pm 5.8	0.5 (15 d)	21 73
Kepone	Adults		0.09 ^a	1	06
Methoxychlor	Adults	4	1.3 (gills) 0.075 (mantle)		39

^amean residueTable 6. Toxicity of tributyltin oxide (TBTO) to hard clam embryos and larvae.¹⁰⁶

Life Stage	Duration hours	LC ₅₀ $\mu\text{g L}^{-1}$
Embryo	24	>1.31
	48	1.13 (0.72-1.31)
Larvae	24	>4.21
	48	1.65
	96	0.015

Table 7. Toxicity of surfactants and syndets to eggs and larvae of hard clams.⁷¹ All values in mg L^{-1} unless otherwise specified.

Compound	LC ₅₀	EC ₅₀
Anionic		
Alkyl Aryl sulfates	1.55 (0.55-3.00)	
AAS-1		5.83
AAS-2		0.98
AAS-3		1.03
Alkyl sulfate	1.22 (0.73-1.46)	
AS-1		0.47
Cationic	0.34 (0.01-1.00)	
C-1		1.27
C-2		0.85 $\mu\text{g L}^{-1}$
Nonionic	2.66 (1.00-5.00)	
N1		0.77
N2		1.75

Table 8. Toxicity of inorganic compounds and heavy metals to various life stages of hard clams.

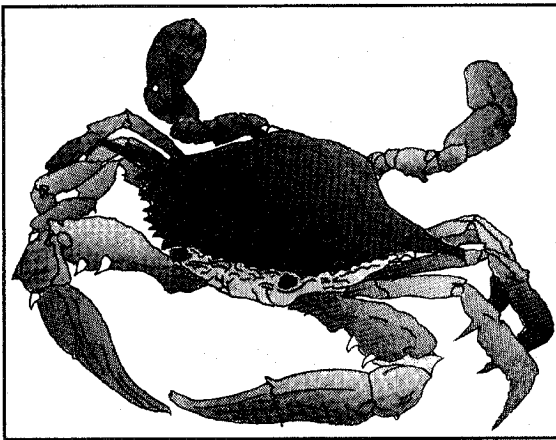
Compound	Life Stage	Test	Concentration, uptake rate, or percent growth	Reference
ammonia	Juv. & adults	96 h LC ₅₀	110-172 mgL ⁻¹	53
nitrite	Juv. & adults	96 h LC ₅₀	81-85 mgL ⁻¹	53
chlorine	Larvae	48 h EC ₅₀	6 gL ⁻¹	107
		48 h EC ₅₀	<6 gL ⁻¹	110
		48 h LC ₅₀	1 gL ⁻¹	107
Ag	Embryo	48 h LC ₅₀	0.021 mgL ⁻¹	28
		48 h LC ₁₀₀	0.045 mgL ⁻¹	28
	Larvae	10 d LC ₅	0.0186 mgL ⁻¹	31
		10 d LC ₅₀	0.0324 mgL ⁻¹	30,31
		10 d LC ₉₅	0.0462 mgL ⁻¹	31
		Growth @ LC ₉₅	66.2%	31
	Adult	96 h Dose	a	30
Cu	Larvae	10 d LC ₅	0.0049 mgL ⁻¹	31
		10 d LC ₅₀	0.0164 mgL ⁻¹	30,31
		10 d LC ₉₅	0.0280 mgL ⁻¹	31
		Growth @ LC ₅₀	51.7%	31
	Adult	accumulation @0.5 mgL ⁻¹	0.06 g kg ⁻¹ d ⁻¹	103
		84 d depletion	50 mg kg ⁻¹ d ⁻¹	103
Fe	Adult	84 d depletion	none observed	103
Hg	Embryo	48 h LC ₅₀	0.166 mgL ⁻¹	28
		48 h LC ₁₀₀	0.0075 mgL ⁻¹	28
	Larvae	10 d LC ₅	0.004 mgL ⁻¹	28
		10 d LC ₅₀	0.0147 mgL ⁻¹	30,31
		10 d LC ₅₀	0.0147 mgL ⁻¹	31
		10 d LC ₉₅	0.0254 mgL ⁻¹	31
		Growth @ LC ₅₀	68.7%	31
	Adult	84 d Depletion	120 mg kg ⁻¹ d ⁻¹	103
Mn	Adult	84 d Depletion	95 mg kg ⁻¹ d ⁻¹	103
Ni	Embryo	48 h LC ₅₀	0.31 mgL ⁻¹	28
		48 h LC ₁₀₀	0.60 mgL ⁻¹	28
Pb	Embryo	LC ₁₀₀	1.2 mgL ⁻¹	28
	Adult	accumulation @0.2 mgL ⁻¹	0.63 g kg ⁻¹ d ⁻¹	103
Zn	Embryo	LC ₅₀	0.166 mgL ⁻¹	28
		LC ₁₀₀	0.25 mgL ⁻¹	28
	Larvae	10 d LC ₅	0.050 mgL ⁻¹	31
		10 d LC ₅₀	0.1954 mgL ⁻¹	31
		10 d LC ₉₅	0.3410 mgL ⁻¹	31
		Growth @ LC ₅₀	61.6%	31

^a0.100 mg kg⁻¹ accumulation in gills increased oxygen consumption.

BLUE CRAB

Callinectes sapidus

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The blue crab is one of the most important species in the Chesapeake. It leads the list of economically important species and would be near the top of a list of ecologically important ones. Bivalves, crustaceans, and fish are its favored foods and blue crabs themselves are important in the diets of striped bass, eels, and numerous other species.

Hatching occurs near the mouth of the Bay in summer and larvae are exported to the continental shelf where development occurs. The number of post-larvae that return to repopulate the Bay each year is greatly influenced by weather conditions on the shelf during the planktonic larval period. Post-larvae that do make it back settle in the lower Bay to metamorphose to the juvenile crab stage.

Juvenile crabs spread throughout the Bay and its tributaries during the fall and the following spring. Submerged aquatic vegetation (SAV) beds and shallow nearshore areas are important nursery, molting, and foraging habitats.

Blue crabs utilize all habitats in the Bay, from the deepest to the water's edge and from the most saline to fresh water. They are most abundant in deeper portions of the Bay during winter, but prefer shallower waters during summer. They may be driven from the water by hypoxic events and mortality occurs in crab pots set in hypoxic water during summer.

Although stocks appear to be thriving, there is concern that overfishing may occur. Shoreline development and contaminant-laden runoff water could degrade important nearshore molting and foraging habitats. Areas that are currently hypoxic in summer could provide additional foraging and living space in the future if conditions improve.

INTRODUCTION

Blue crabs are currently the most economically important species in the Bay. The annual harvest of hard crabs from the Chesapeake accounts for more than 50% of U.S. landings. They also play a significant role in the ecology of the Bay because they are so abundant, eat so many different components of the system, and are important in the diets of numerous other species. The population of blue crabs in the Bay, as measured by commercial landings, varies in

size from year to year. In the long term catch record, there is no indication that the population is declining, but there is concern that increased fishing pressure may cause declines similar to those seen in other commercially important Chesapeake Bay species.

Current concerns for the future of blue crabs in the Bay include potential overfishing, loss of nursery and molting habitat in submerged aquatic vegetation beds and in shallow unvegetated near-shore areas, and reduction in

summer habitat area due to hypoxic conditions in deep waters. The Fisheries Management Plan for blue crabs, developed under the Chesapeake Bay Agreement, addresses the issues of potential overfishing and habitat loss. Blue crabs have been studied extensively for nearly a century and the scientific literature on this species is vast. A number of classical reviews of its biology and fishery in the Chesapeake area were published between 1905 and 1987.^{20,44,92,98,107,140,143,144,145} An annotated bibliography on the fishing industry and biology of the blue crab abstracted 742 publications predating 1970.¹³⁷ Two U.S. Fish and Wildlife Service "Species Profiles" were published on the blue crab during the last decade, one for the South Atlantic states and the other for the Gulf of Mexico^{108,142}. Most recently, in early 1990, a special issue of the *Bulletin of Marine Science* was devoted to papers on the blue crab.

BACKGROUND

The blue crab is a decapod crustacean in the family Portunidae. Like other members of this family, the blue crab is a swimming crab. Mature males as large as 9 in (227 mm) have been recorded from the Chesapeake Bay. Females vary considerably in adult size, ranging from 55 to 204 mm in carapace width. Blue crabs inhabit depths from the water's edge to 90 meters but are most abundant in depths less than 35 meters. The original geographic distribution of this crab was from Nova Scotia to northern Argentina but the species has been introduced to Europe and the Mediterranean Sea and has been reported from Japan.^{155,156} Along the coasts of the U.S. the blue crab is found in abundance from Texas to New Jersey. Although the Chesapeake has been the major producer of commercial blue crabs, it is clear from its distribution that the species can adapt to a variety of habitats.

During the course of its life, the blue crab utilizes all habitats within the Chesapeake Bay. Mature females migrate to the high salinity waters near the mouth of the Bay where spawning occurs during the summer months. Newly hatched larvae swim to the water's surface where they are swept out of the Bay by surface currents. Larval development is completed in continental shelf waters and the survivors return to the Bay as post-larvae and early juveniles in late summer and fall. Juveniles disperse throughout the Bay and its tributaries, where growth and maturation occur. The young crabs require 14 to 18 months to reach adulthood and do not grow during the winter months. Crabs tend to be most abundant in the shallower areas of the Bay during warm weather, and are plentiful in the deeper portions during the winter months.

Distribution

The distribution of blue crabs in Chesapeake Bay varies with age and sex of the crabs and with season. In a bay-wide trawl and dredge survey, Lippson^{72,73,74,75} found

that during winter, juvenile blue crabs having a modal size of 25 mm were concentrated on muddy bottoms, in water 35 to 50 ft (12-17 m) deep in mid-bay. Few juvenile crabs were found north of the Choptank River or upstream of river mouths during the winter months, but by June, they had scattered and occupied rivers and tributaries throughout the Bay. Densest concentrations in June were still in the mid-bay region but included the Choptank River. The highest concentrations of juvenile crabs in Virginia waters were in the rivers.

A Bay-wide survey in May, 1969, found crabs as far north as Pooles Island near the head of the Bay for the first time since the previous November. Juveniles were still abundant in the deeper waters at Cove Point during May but the pattern of depth preference reversed during June and almost no juveniles were found in water deeper than 30 ft (10 m). During the period from mid-July to mid-October, large numbers of adult crabs were found throughout the Bay and its tributaries. There were even large numbers of crabs in the upper Bay as far north as the Susquehanna River flats. Lippson reported that there were record numbers of blue crabs in the Bay in 1969 and that in the fall, large numbers of crabs in poor condition (perhaps because of limited food) moved out into deeper water and muddy bottoms as water temperature decreased.

During February, 1970, the mid- and lower Potomac River was sampled. Many adult crabs were found but few juveniles were present. Large numbers of sub-adult juveniles (60-90 mm) were present in the Cove Point region during November to January along with smaller numbers of the new year class in the 20 to 30 mm size class. In April, a smaller size class (11-20 mm) of juveniles was found moving up-Bay through the Cove Point region. Winter mortality was reported to be 19.3% in the Cove Point region, considerably higher than the 3.3% found the previous winter. Water temperatures were similar during both winters and Lippson felt that the poor condition of the overwintering crabs contributed to the higher winter mortality.

The new year class was detected in Tangier sound in August of 1970; they were also present in the Patuxent River and at Cove Point. A survey of Pocomoke Sound, Tangier Sound, and the Pocomoke, Nanticoke, and Wicomico Rivers during September found the highest concentrations of juveniles in salinities ranging from 12 to 18 ppt. During the same time, adults were most abundant in lower salinities of 10-14 ppt.

Recruitment of the new year class to shallow areas near Solomons, Maryland began in early August of 1970 and reached a peak in late September and early October. By November 1, the numbers in shallow water declined rapidly and it was found by dredging and scuba observa-

tions that the young crabs had moved to mud bottoms in deep water.

During the summer, the C&D Canal was occupied by low densities of juvenile crabs, mostly males. During winter and early spring, the catch in the Canal and nearby Bay sites was zero or nearly so. Salinity in the Canal ranged from 0.6 to 2.3 ppt during the period from March 1971 through August, 1972 and males outnumbered females by about four to one during this period. Sampling in Tangier Sound during August of 1971 and 1972 produced 3.8 and 8.7 times the catch of blue crabs in the C&D Canal during the same month. The authors concluded that the C&D Canal was not a significant avenue of exchange of blue crabs between Delaware Bay and Chesapeake Bay.⁹⁰

In a 14-year study at Calvert Cliffs in mid-Chesapeake Bay, Abbe¹ found that the number of female crabs in his samples continued to increase throughout the season (May to October) and were more numerous than males in September, October and November. He found a peak catch in his pots in October, which he attributed to migrating females moving to the lower Bay for overwintering and spawning. Of the 57,078 crabs caught during his study, 51.5% were males.

The winter dredge fishery is confined almost entirely to water deeper than 9 meters from Cape Henry to the Wolf Trap light, but some winter dredging has been done from Wolf Trap north to the Maryland state line.⁸¹ The overwintering population is joined in the spring by mature females migrating to the lower Bay to spawn,⁵⁶ which suggests that some mature and nearly mature females overwinter in mid-Bay areas and/or in the deeper portions of rivers. In New Jersey bays, winter dredging is done in waters only 2-3 meters deep. As in the Chesapeake, the catch is largely mature females (85%).⁴¹ In Chincoteague Bay, adult female crabs tagged in the fall were recovered close to their release site following summer.¹⁶ Since Chincoteague Bay is very shallow (maximum 2.3 m), it is clear from these two studies that mature females do not require deep water to overwinter successfully.

A recent study of the distribution and abundance of overwintering blue crabs in the lower Bay found that crabs were more abundant in water deeper than 9 m where sediments contained 40-80% fine silty sand. Crabs were less abundant in both coarser sediments and finer sediments. In high energy spit and shoal areas, characterized by highly mobile sandy sediments, crabs were rare or absent. They were most abundant in basin areas, least abundant in shoal areas and intermediate in abundance in channels. Mature females accounted for 90-98% of the catch in this study.¹¹⁸

Population Status and Trends

The blue crab population, as measured by commercial harvest, has varied greatly over the 110 year history of the fishery. There is a general upward trend in the catch record that probably reflects increasing fishing pressure rather than increasing abundance of crabs. So far, the crab population appears to be sustaining itself in the face of increasing fishing pressure and changes in the water quality and ecology of the Bay. However, there is increasing concern by biologists, managers, and watermen that the blue crab may become overexploited by increasing fishing pressure.

Commercial fishing for crabs includes capturing "peelers" 3.5 inches (85 mm) or larger for crab shedding operations, hard crabs of both sexes larger than 5 inches (121 mm), overwintering crabs that are mostly mature females, and egg-bearing females in the summer in Virginia waters. In addition to the commercial catch, there is a large recreational catch each year. This level of exploitation led Truitt to write of the blue crab that "Few animals, indeed, could withstand such drafts upon them at all seasons of the year while breeding, while carrying eggs, while molting, while hibernating, and while in the several stages of growth".¹⁴⁰

Historically, years of poor catch have caused alarm, and overfishing and wastage in the industry have been blamed. As long ago as 1924 Maryland crab packers predicted annihilation of the industry and, Dr. Radcliff, the Deputy U.S Commissioner of Fisheries recommended that Virginia should prohibit catching sponge crabs, and should shorten the winter dredge fishery from 6 to 3 months. He also recommended that both Maryland and Virginia should increase the legal size of hard crabs from 5 to 6 inches (121 to 145 mm) and Maryland should increase the legal size of soft crabs from 3 to 3.5 inches (72 to 85 mm). Both states were encouraged to prevent the taking of green peelers for shedding because most of them died.²⁹

Similar recommendations have been made from time to time when the catch has been lower than in previous years,^{98,107,140} and the 1989 Fisheries Management Plan for Blue Crabs contained the same recommendations that Radcliff set forth in 1924.

In 1948, Pearson concluded that changes in abundance of crabs were due to natural causes and suggested that varying annual rates of survival of young crabs prior to the time they entered the fishery were responsible for fluctuations in the catch. He could not find a correlation between winter air temperature and the series of fluctuations in annual abundance of crabs between 1930 and 1944. He did, however, write that the volume of discharge of the James and Potomac Rivers during the spawning season of the blue crab was negatively correlated with the index of annual abundance of adults taken in the second winter

after hatch. This led him to suggest that abundance of crabs was related to river flow.¹⁰⁷ The fact that tropical storm Agnes turned most of the Bay to fresh water in June of 1972, but had no apparent effect on the catch of crabs in the following years, tends to discredit Pearson's river flow hypothesis.

Biologists today generally agree that large annual fluctuations in abundance of crabs are likely due to variable weather conditions on the continental shelf during the planktonic larval phase of the life cycle. Unfavorable conditions may carry large numbers of larvae away from the Bay and result in poor crab years, whereas favorable conditions may bring large numbers of megalopae back to the Bay, resulting in good crab years a year or two later.

Until recently, no relationship was evident between the size of the spawning stock and subsequent recruitment of blue crabs.^{107,131,145} However, a recent analysis of fishery-independent trawl data from the York River covering the years 1972 to 1988, and a re-analysis of Pearson's data, has shown that both a stock-recruitment relationship and a recruit-stock relationship exists for the blue crabs of the Chesapeake Bay.⁷⁰ In other words, when spawning stock size is large, more juvenile crabs are recruited, and higher numbers of juvenile crabs result in a larger spawning stock. These simple relationships are masked by abiotic factors affecting recruitment of postlarvae and biotic factors causing varying survival of newly recruited young such as predation, food availability, and cannibalism.

LIFE HISTORY

After mating, mature females, known as sooks, migrate to the lower Bay in large numbers in late summer and fall. These females overwinter in the deeper basins of the lower Bay and are joined in the spring by more females whose migration was interrupted by cold weather in the fall. In the spring, eggs are fertilized by sperm stored over winter by the females. The fertilized eggs are extruded and attached to fine hairs on the abdomen. A female may carry 750,000 to 8,000,000 eggs and is called a sponge crab.¹¹⁰ Eggs are carried about two weeks before they hatch and a female may spawn more than one time. Hatching occurs from June through September.¹⁴³ The newly hatched larva is called a zoea and looks nothing like the adult crab. The zoea swims near the surface of the water and molts six or seven times to progressively larger stages. At the last larval molt the zoea metamorphoses into a post-larval form known as the megalops. The megalops has claws like a crab and is a strong swimmer but it also can crawl on the bottom. Eventually the megalops settles and metamorphoses to the first crab stage which looks much like the adult blue crab but is only about 2.5 mm from point to point. Development from hatching to the first crab stage may take from 45 to 60 days or more, depending on temperature, during which time the larvae may be trans-

ported great distances in the surface waters of the Mid-Atlantic Bight.¹³⁰

Little more than a decade ago, it was widely accepted that the large spawning population in the Chesapeake Bay produced larvae which developed within the Bay and became the juveniles of the new year class. However, Sandifer found no evidence for retention of blue crab larvae in Chesapeake Bay and he suggested that recruitment was probably from immigration of post-larvae and juveniles from coastal waters.¹¹⁷ Researchers in other geographic areas also had evidence that larvae were not retained near their spawning grounds. South of Cape Hatteras two separate studies reported larvae as far as 64 km offshore.^{28,99} Tagatz concluded that although early development occurs within a few km of shore in Florida waters, growth after the second zoeal stage takes place farther offshore and at least some blue crab larvae return to inshore waters as megalopae.¹³³ Biologists in Texas also found that zoea larvae developed offshore and megalopae of blue crabs reinvaded bays and coastal estuaries.^{58,93} This postlarval stage may penetrate far into estuaries before metamorphosing into a juvenile crab. In a long term study of North Carolina estuaries, Williams found blue crab megalopae as far as 80 km inland from the nearest ocean inlet and emphasized that dispersal during this postlarval stage was substantial.¹⁵⁴ In the Chesapeake, megalopae penetrate as far as Tangier Island [unpublished data: R. Orth, Virginia Institute of Marine Sciences (VIMS)] before metamorphosis, and rarely, as far as the Patuxent River.¹⁷

In 1978, a broad program of research was initiated under the auspices of the Office of Sea Grant to determine the true source and mechanism of recruitment of blue crabs to Mid-Atlantic Bight estuaries. The program was conducted by investigators at the University of Maryland, the University of Delaware, and Old Dominion University. It involved extensive and intensive field sampling to determine vertical and geographic distributions of various larval stages with respect to Chesapeake and Delaware bays, experimental studies on behavioral adaptations and dispersal mechanisms of larvae, and descriptions of physical oceanography of the system in which larvae are dispersed. Findings of these investigations have been summarized in a number of publications.^{7,85,124,128}

Laboratory studies showed that first stage larvae possessed behavioral traits that would bring them to the surface and that early larvae would thus be transported out of the estuary with the surface waters.¹³² Field studies confirmed that stage I zoeae were found predominantly in surface waters in the mouths of both Chesapeake Bay and Delaware Bay.^{27,35,111} Later zocal stages were found offshore and remained in surface waters.^{34,86}

Although circulation patterns on the shelf are dominated by a mean southward flow of water, larvae may be retained near the Chesapeake by prevailing southwesterly winds during summer which can produce a band of northerly flowing water on the inner shelf.⁶ Movement back to parental estuaries appears to occur during the megalops stage,⁵³ but the mechanism for transport has remained unclear.^{35,54,55}

Duration of the megalops stage is greatly prolonged by decreased temperature. Megalopae could therefore use the slow on-shore residual drift, in cool bottom waters, for transport back to the mouth of Chesapeake Bay.¹³⁰ Once near the estuary mouth, megalopae may be using tidal flow to re-invade the estuary. In the laboratory, blue crab megalopae respond to changes in hydrostatic pressure by swimming faster and upward,^{94,129} a behavior which could provide a mechanism for using tidal currents for transport. In the field, megalopae were absent from the water column on ebbing tides but present in samples taken during flood tides.³⁵ The hypothesis that megalopae enter estuaries by rising into the water column on flooding tides has been supported by further field studies.^{13,76}

A recent study presented evidence that megalopae near the mouth of the Bay are transported into the Bay during wind-forced inflow events that bring large volumes of shelf water into the bay (positive volume anomalies). During the 1985-1987 recruitment seasons, 12 of 16 pulses of megalopal settlement at the VIMS pier occurred during positive volume anomalies. The largest settlement event in 1985 was associated with Hurricane Juan which moved about 8 km³ of shelf water into the Bay. Although that was the largest storm surge in 28 years, the authors reported that positive volume anomalies occurred during the normal period of megalopal recruitment an average of 10 times each year. The authors suggested that because it is virtually certain that several major inflow events will occur during the season when megalopae are present, these events may represent one of the most important pathways for reinvasion of the Bay by megalopae. Because the inflow events are highly variable in timing, number, and intensity from year to year, they may account for a large part of the variability of megalopal recruitment and ultimately, recruitment to the adult population.³⁹

Sulkin and Epifanio¹²⁸ concluded that because the major factors regulating year-to-year variation in recruitment success are most likely physical, hydrographic ones, "... namely, flow reversal in summer and onshore surface flow in fall . . .", measurements of spawning stock size or measurements of larval abundance on the shelf are unlikely to provide useful predictions of future harvests. They went on to propose that "The earliest point in the life history providing a reliable measure of year-class strength is the appearance of post-metamorphic juveniles in the lower estuary."

Recent research at VIMS has focused on daily, seasonal, and annual variations in abundance of megalopae and post-settlement juvenile blue crabs, and the nursery functions of different habitat types near the mouth of the York River. There is evidence that megalopae settle preferentially in grass beds when they are present.¹⁰³ Continuous low level settlement of megalopae occurs from August through November at the mouth of the York River at temperatures ranging from 7 to 31°C. However, most of the settlement during a four year period occurred between September 24 and October 6. Peaks of settlement activity ranging from 1 to 3 days occurred each year and coincided with the full moon. The largest settlement events occurred during different times each year, ranging from early September to early November.¹⁴⁷ Settlement events were correlated with availability of megalopae in the plankton and more megalopae were nearing the molt to the crab stage upriver than at the mouth. Megalopae collected from the bottom were also closer to molting than those in the plankton.⁷¹ Densities of planktonic megalopae varied in both time and space, with large variations occurring at sites separated by a few hundred meters.

In the middle Chesapeake Bay region, Lippson⁷⁵ and Sulkin¹²⁷ studied juvenile recruitment but not the relative importance of habitat types. Sulkin found that recruitment to Tangier Sound began in September and October and additional movement of young-of-the-year crabs continued into the following summer. Recruitment of the new year class occurred 2 to 4 weeks earlier at Smith Island and Crisfield than in the Potomac and Patuxent Rivers and in some years when cold weather intervened, small crabs did not appear at the latter sites until the following spring. Sulkin hypothesized that transport of denser, more saline water toward the Eastern Shore (the Coriolis effect) might account for the earlier appearance of juveniles in Eastern Shore waters than in Western Shore rivers. Sulkin may have missed late fall arrivals because his sampling did not extend past early October in most years. Recruitment of the new year class can continue into November in the upper Bay as far north as Annapolis.⁴⁸

As water temperature drops in the fall, the young crabs become less active and finally cease feeding as the temperature drops below 10°C or so. The small crabs burrow in the bottom, especially during daylight hours,⁸¹ and overwinter in shallow grassbeds, shallow muddy bottoms, and in the deeper waters in mid-Bay.^{75,105,139} Little or no growth occurs from December through March, but when the temperature rises in the spring, the little crabs become more active and begin feeding, growing and dispersing further into the rivers and tributaries and into the upper Bay.

Crabs entering the Bay as megalopae in August and September may reach adulthood by late summer or fall of the next year. Those arriving as post-larvae in October and

November will probably spend their second winter as large juveniles and reach adulthood the following spring and summer. Newly settled crabs molt every few days when the weather is warm, but as they increase in size, the length of time between molts increases. About 18 molts are required to reach adult size.

A female approaching her final molt is carried by a male until she molts. After molting, while she is still soft, mating occurs. After mating, the male continues to carry the female until her shell hardens. The female then migrates down the Bay to the high salinity waters to spawn. If she has matured early in the summer she will spawn before summer ends and may overwinter to spawn again the following spring. Females maturing late in the summer or fall will overwinter before their first spawning.^{19,140} Although it is generally accepted that females do not molt after reaching maturity, there is recent evidence that some females may molt again.⁴³

Mature males may molt several times after reaching sexual maturity. In contrast to the females, males do not migrate to the lower Bay but remain in the upper portions, migrating to deeper waters to spend the winter months. Few crabs live longer than three years.

ECOLOGICAL ROLE

Predators

The larval and post-larval stages of blue crabs are probably preyed upon by a variety of small fish and gelatinous zooplankton while in the plankton. After settlement, megalopae may be preyed upon by grass shrimp, sand shrimp,¹⁰² juvenile blue crabs, and a variety of fish that feed in nursery areas.

American eels are major predators on blue crabs. In the lower Bay, blue crabs made up 33-68% of the total volume of food in stomachs of eels from the James, York and Rappahannock Rivers.¹⁵² American eels were also predators on blue crabs in New Jersey sea grass beds.¹⁵⁷

Striped bass may also consume large numbers of small blue crabs. One study found that striped bass longer than 25 cm contained up to 20-25 small blue crabs each.¹⁴¹

Numerous authors have reported that larger blue crabs prey on smaller blue crabs.^{19,23,48,64,133} Cannibalism may account for as much as 90% of the mortality of juvenile blue crabs in the Rhode River (personal communication: A.H. Hines, Smithsonian Environmental Research Center, Feb. 23, 1990).

Other predators known to eat blue crabs include Atlantic croakers, cobia, red drum, black drum, oyster toadfish, sand bar sharks, bull sharks, cownose rays, speckled trout, weakfish, catfish, gars, largemouth bass, loggerhead

turtles, Atlantic ridley turtles, herons, egrets, diving ducks and raccoons.^{3,23,92,108,145,157}

Food

Newly hatched blue crab larvae are very small and require very small food items. In the laboratory, they can be reared through the first several molts by feeding them rotifers and/or larvae of polychaete worms. After they have molted twice, they are large enough to eat freshly hatched brine shrimp larvae. In the field, they probably eat rotifers, larvae of various worms and copepod nauplii when they are very small, and adult copepods may be a main food item as the zoeae grow larger.

Although the blue crab has been characterized as a scavenger in the past, studies on feeding habits of blue crabs show that it is also a voracious predator that is very likely responsible for controlling populations of some bivalves and fish. Because it is highly cannibalistic, the blue crab may also control its own population density to some extent. Blue crabs have even been observed to rush out of the water to catch fiddler crabs in the exposed salt marsh,^{47,51} and reach out of the water as much as 7 cm to pick marsh periwinkles from the stems of cordgrass.⁴² In addition to being predatory, blue crabs also consume plant matter and detritus, especially when they are small. The diet of blue crabs varies with the size of the crab, habitat that it lives in, and season of the year. In Table 1 the results of four studies of the diet of blue crabs are summarized.

One study reported that young blue crabs fed primarily in the early morning or at night whereas the stomachs of adult crabs were fullest in mid-afternoon,²³ but another study⁶⁴ found no day-night differences in total food consumption in subtidal habitats. In a 24 h study comparing feeding of 60-130 mm crabs in a marsh creek and seagrass bed, feeding was related to tidal cycle in the marsh creek. Overall stomach fullness of crabs in the grassbed was higher than in the marsh creek, probably because feeding could continue through all tidal cycles in the grass bed.¹¹⁴ Using an ultrasonic tag that emitted a special signal when a crab was feeding, Wolcott and Hines found that a crab exhibited 2-7 feeding bouts per day. During the 96 h period when the crab was tracked in the Rhode River, no diel or tidal pattern of feeding was evident.¹⁶⁰

Detritus formed 19-27% of the diet by volume of crabs measuring 30-194 mm in Lake Pontchartrain, Louisiana. The proportion of mollusks in the diet of crabs increased from 34% in 30-74 mm crabs to 63% in the largest crabs. Crabs and other crustacean remains formed a declining portion of the diet as crabs increased in size, ranging from 36% of the diet of the smaller crabs to only 10% of the diet in larger crabs. Fish were not important in the diets of small crabs, but in larger crabs, they formed as much as 5.4% of the food consumed. Vegetable matter was impor-

tant (12% of volume) in only one size group of crabs measuring 75-124 mm.²³

Blue crabs would eat amphipods in an aquarium, but were less efficient predators on amphipods than two species of shrimp and several fish species. But, in another study, the same author found that his experiments with blue crabs were equivocal. In the lab, a significant decrease in total macrobenthos occurred but in field inclusion cages, total macrobenthos increased, due primarily to large increases in amphipod abundances. In the field, only the numbers of two snail species decreased in cages that included a blue crab. Further analysis of these data showed significant reductions in abundance of five species of polychaetes in laboratory experiments but not in field experiments.^{95,96,97}

Another researcher found that blue crabs ate a variety of polychaetes in the York River and that soft-shelled clams, coot clams and other clams were nearly eliminated by blue crabs and spot. He concluded that polychaetes and bivalves living near the surface were most vulnerable to crab predation and that blue crabs probably controlled the size of the population of bivalves during the warmer months.^{148,149} Similar findings were reported from predator exclusion studies in the upper Chesapeake bay.⁵⁰

In laboratory studies, blue crabs measuring 70-74 mm in carapace width ate an average of 18.8 small Atlantic ribbed mussels per day over a 7 day period. Crabs chose smaller mussels when a range of sizes was available. About equal preference was shown for all mussel sizes below 2.5 cm, a size that is easily crushed by blue crabs. In short term experiments crabs showed no preference for Atlantic ribbed mussels over another species (*Brachidontes*) but preferred the former over oysters of similar size.¹²² Small to medium sized crabs in the Newport River estuary (North Carolina) appear to specialize on Atlantic ribbed mussels. The crabs follow flood tide into the oyster-mussel zone and feed until the tide recedes.⁵¹ Intertidal predation on another species, the blue mussel, was observed in New Jersey.¹⁰⁹

In intertidal marshes, blue crabs exhibited a distinct species preference for the marsh periwinkle. Intermediate size classes of the snail were preferred over larger and smaller ones. Killifish also were preyed upon by blue crabs in the marsh, and crabs selected large fish as was found also by another researcher⁵⁹ who concluded that the blue crab was the major predator on adult mummichogs in the marsh. The Atlantic ribbed mussel was not a preferred prey in this study, and there was no evidence of size selection for this prey.¹⁵³

Over 4,000 blue crab stomachs from the Apalachicola estuary in Florida were examined.⁶⁴ Pooled data from all sizes, dates and stations are summarized in Table 1. The

remainder of items found, including ostracods, insect larvae, polychaetes, mysids, amphipods and other items, each accounted for less than 1% of the diet.

Clear differences in diet between size groups of blue crabs were found in this study.⁶⁴ Although bivalves were by far the most important food for all three size groups, juveniles measuring less than 31 mm in carapace width ate more plant matter, ostracods, and detritus than the larger size classes. Fishes, gastropods, plant matter and xanthid crabs were important components of the diet in the middle size range (31-60 mm), whereas fishes, xanthids, and blue crabs ranked highest in the diets of crabs larger than 60 mm.

Seasonal and spatial differences in diet were most evident in the smaller crabs and were related to habitat and seasonal availability of prey. The author concluded that "... all crabs utilize whatever food items are locally available at any time ..." and that because the species feeds upon almost every dominant food item in the system, blue crabs are a crucial factor in the food web and may play an important role in determining abundance and fluctuations of many of its prey. He cautioned that because they were omnivorous, detritivorous, cannibalistic and scavengers, it is difficult to place them at any one trophic level. In addition, because of the ontogenetic changes in diet, he suggested the use of "trophic stages" in food web models and noted that the food web should be treated as dynamic and flexible in time and space.⁶⁴

In a study of the diet of blue crabs from bays and marshes in Texas, all crabs were caught nearshore during daylight hours. The author concluded that in these shallow, nearshore habitats, blue crabs occupied detritivore, omnivore and primary carnivore trophic levels.²

In contrast to other studies, this study found that plant material formed a significant portion of the diet of blue crabs. Small crabs measuring less than 31 mm carapace width utilized vascular plants, algae and foraminifera more than the mollusks, fish and crustaceans found in crabs larger than 60 mm. The large amount of plant material in the diet of these crabs was attributed to the fact that 73 % of the animals were collected along salt marsh and brackish marsh shorelines. Other authors found lesser quantities of plant material in crab diets.

An ontogenetic trend of increasing predatory behavior with increasing size of blue crabs was found in another study. Detritus formed an important component of the diet in crabs 10-60 mm in carapace width. Crabs and bivalves were the most important dietary items in the largest crabs (126-150 mm). Amphipods, polychaetes and foraminiferans were important in the diets of the smaller crabs but not in the diets of crabs larger than 60 mm.¹²⁶

Large soft-shelled clams attain a partial refuge from blue crab predation by deep burial, but size or shell strength did not afford protection from blue crabs.^{4,5} Predation on large (48-60 mm) clams by adult blue crabs was lower in sandy substrates than in mud, and predation was lower in sand at low densities than at higher densities. These authors reported that blue crabs became satiated after eating an average of 8.25 clams in 72 hours.⁶⁹ About 50% of the diet of blue crabs in the Rhode River is composed of soft-shelled clams and Baltic clams.¹⁶⁰

Another example of the blue crab's voracious appetite was a study that found that large male blue crabs could eat up to 142 small (15 mm shell height) oysters per crab per day. As many as 27 oysters measuring 25 mm each could be eaten by a crab in a single day. The author concluded that predation by large male blue crabs could lead to local extinction of juvenile oysters in this size range.³⁰

Because of its varied diet, the blue crab has many competitors. For example, American eels, spot, mud crabs and canvasback ducks are just a few of the organisms that also prey on clams, one of the major items in the diet of blue crabs. Changes in abundance of these, and other, competitors will very likely affect the population of blue crabs.

HABITAT REQUIREMENTS

Water Quality

Dissolved Oxygen

Blue crabs generally avoid areas with low dissolved oxygen concentrations. They may even leave the water in large numbers to escape hypoxic water. In the Chesapeake, these events, when crabs emerge from the water, are known as "crab wars"; in Alabama, such events are termed "jubilees". The catch of crabs in pots set in hypoxic water is generally much lower, or near zero, than in water with adequate oxygen (personal communication: W. Goldsborough, Chesapeake Bay Foundation) and crabs in pots in hypoxic waters are often dead when the pots are pulled.

Carpenter and Cargo¹⁸ found that a pO_2 of about 50 mm mercury (32-36% of saturation) is lethal to animals in pots that cannot escape. They found about 50% mortality or more in crab pots when oxygen was less than 2.0 ppm below 7 m depth.

Hypoxic conditions occasionally occurred at Kenwood Beach, on the Western Shore in mid-Bay, in 3-10 m of water during July and August. The episodes lasted for 1-3 days and oxygen concentrations ranged from 0.1 to 3.0 mgL^{-1} . During these periods, the catch was much reduced and crabs in the pots were dead or nearly so.¹

Officer *et al.*¹⁰¹ reported that watermen from Tilghman Island said that before 1965 crabs were abundant in deep water (> 20 m) prior to mid-May and after mid-September but that there was no longer any deep water crabbing. During the summer of 1982 no crabs were caught in water deeper than 4 m. Citing a personal communication from A.C. Carpenter, (Potomac River Fisheries Commission) these authors reported that all crabs below 6 m in the lower Potomac died in 1973 and that crabs were driven ashore in large numbers in many late summer periods. Reports of "crab wars" in which tens of thousands of crabs crowd into shoal waters and may actually leave the water were also cited for the mid-Bay region. They noted that anoxia may reduce the food supply of benthic feeders, crowd them into a smaller volume and exclude them from the food supply and space previously available.

One study determined LC_{50} values for juvenile crabs measuring 28-54 mm at a salinity of 10 ppt. The 28 day LC_{50} was 79% of saturation at 30 °C. The seven day LC_{50} was 65% of saturation at 30 °C.¹²⁵ These are relatively high oxygen concentrations, suggesting that there may have been problems with these experiments. The LT_{50} to anoxia was less than one day at 20 and 30 °C, which seems reasonable.

In contrast to these findings, de Fur *et al.*²⁶ had less than 20% mortality in 23 and 25 day experiments of continuous exposure to 50-55 mm of mercury (35.5-39% saturation). There was no mortality in seven-day experiments at this level of hypoxia. Temperature was 21-23 °C and salinity was 500-530 mOsm (roughly 15 ppt) in these experiments. Crabs became active when pO_2 fell to 50 mm mercury, but became quiescent for the duration of the hypoxic exposure. Another study also reported that crabs became active when exposed to hypoxia (< 0.5 ppm) and remained active for 10-30 minutes before they became quiescent and eventually moribund in 2 h at 32°C and 4.3 hr at 25°C. Moribund crabs would die if not returned to normoxia within 10-15 minutes.⁷⁹

Salinity

Blue crabs inhabit all regions of the Bay from the high salinity region at the mouth to tidal fresh waters^{36,25} but they are most abundant in waters of intermediate salinity. Larval blue crabs are much less tolerant of low salinity and must be in water having a salinity greater than 20 ppt in order to survive. In the laboratory, larvae survive in the highest numbers at a salinity of 30 ppt.²²

Turbidity

No information was found on the effects of turbidity on blue crabs. Very turbid water might interfere with swimming of the tiny first larval stages found in the mouth of the Bay during summer, but detrimental effects on juvenile and adult crabs seem unlikely.

Temperature

The 48 h temperature tolerance limits of blue crabs acclimated for 21 days to four temperatures and two salinities have been determined. Tolerance of juveniles and adult females was similar and was decreased by lowered salinity. The upper temperature limit of crabs acclimated at 30°C and 34 ppt was 39°C and the lower limit of these crabs was 4.6-4.9°C. Crabs acclimated at the low salinity (6.8 ppt) and 30°C had upper limits of 37°C and low limits of 5.3-6.0°C. At the lowest acclimation temperature of 6°C, the low temperature tolerance limit was less than 0.0°C. Crabs acclimated at this low temperature and either 34 ppt or 6.8 ppt had upper tolerance limits of 33°C and 31.5°C respectively.¹³⁵

Blue crabs exhibited a wide range of temperature preference in a power plant cooling pond. Crabs appeared to choose the warmest temperatures and exhibited no preference for a specific temperature range. The largest number of crabs were captured in areas of the pond where temperature ranged from 35.0 to 37.4°C. At the extreme high temperature of 41.8°C, most crabs captured in pots were moribund or dead.⁶⁸

In a laboratory study of the effects of low temperature, locomotor activity of juvenile crabs ceased when water temperature fell to 5.5°C. When temperature was elevated to 12.5°C, nine days later, crabs again became active.¹⁴⁶

In long term survival tests, Van Heukelem and Sulkin (unpublished) found that juvenile crabs (less than 15 mm) could survive 1°C for 30 days at salinities of 10 and 20 ppt. Only about 50% survived for 30 days at 1°C and 5 ppt; more than 40% died in 20 days at 3°C and 5 ppt; and there was more than 50% mortality in 20 days at 3°C and 2.5 ppt. These results and those of Tagatz¹³⁵ demonstrate that blue crabs are less tolerant of low temperature at low salinities. Thus, in areas of low salinity, the migration of juvenile crabs to deeper water during cold weather has survival value.

Low commercial catches have been blamed on winter mortality due to unusually cold winters in a number of cases. According to Krantz,⁶² Leidy made the first observations of winter mortality in 1888. The poor commercial harvest in 1902 was attributed to the severe winter of 1901-1902.¹¹² Large numbers of dead crabs occurred on winter dredge vessels in two of the coldest winters on record (1917-1918, and 1939-1940).¹⁰⁷

During the Bay Ice Team Effort (Project BITE), surveys in February and March following the severe winter of 1976-77 revealed that the combined total mortality of immature and mature crabs at all 128 stations sampled was 48%. Generally, mortality was more severe in shallow water (< 50 ft) than in deeper water and was more pronounced on the Eastern Shore than on the Western Shore. Adult

crabs were more prone to winter mortality than immature crabs [< 5 inches (121 mm)]. Although landings of adult crabs were depressed in early spring through mid-summer, examination of catch records shows that the total catch for the Bay for 1977 and again for 1978 was higher than for 1976. In the BITE report, Sulkin noted that although Lippson⁷⁵ reported the highest winter mortality in 1970 of a four year period, the highest soft crab landings and the second highest hard crab landings of that period occurred in 1970.⁶² Thus, there appears to be little relation between winter kills of blue crabs and subsequent harvest.

Although it has been generally accepted that all blue crabs migrate to deeper water as the water temperature drops in the fall, juvenile blue crabs have been found to overwinter in shallow water habitats in lower Chesapeake Bay, New Jersey, and Texas.^{105,139,159} It is also generally accepted that crabs remain buried and inactive during the winter months. However, one study has shown that crabs buried in response to light at low temperatures but moved around and even fed to some extent in the dark. This study also noted that Truitt found that overwintering females in the lower Bay moved about in schools.⁸¹

Suspended Sediments

In some flowthrough crab shedding systems silt may build up and clog the gills of crabs, resulting in mortalities.⁴⁹ No information was found on the effects of suspended sediments on crabs in the field.

Nitrogen

In closed crab shedding systems, ammonia and nitrite can reach levels that are toxic to crabs. Ammonia levels should be kept below 1.0 mgL⁻¹.⁴⁹ Nitrite concentrations below 0.5 mgL⁻¹ are considered safe for shedding crabs. Levels of nitrite between 0.5 and 3.0 mgL⁻¹ are associated with moderate mortalities in shedding crabs; concentrations between 3 and 10 mgL⁻¹ cause chronic mortality; and levels above 10 mgL⁻¹ are acutely toxic even to intermolt crabs.⁸²

pH

Blue crabs showed a marked avoidance reaction to acidic (pH 4.6 and 5.8) runoff from clear-cut timber areas and to water of low pH in the laboratory. In these studies, there was an inverse relationship between pH and avoidance in the range of pH 4.5 to 7.0. In the field, however, small crabs were more abundant during periods of high runoff and low pH than at other times during a long-term sampling program.⁶⁵

Structural Habitat

Grass beds are important nursery habitats for juvenile blue crabs^{45,46,105} and peak densities of 50-90 juveniles per square meter have been reported by several authors.^{91,103,105,139} The highest reported densities in grass

beds were for the smallest size classes (< 11 mm) and, like the abundance of megalopae, the numbers of these smallest crabs varied greatly from year to year and site to site. Abundance of larger juveniles was much more uniform from year to year and from site to site within grassbeds, suggesting high mortality of the smallest crabs and/or migration out of the grass beds after attaining larger size.

Abundance of juvenile blue crabs was only about one tenth as great in a nearby marsh creek as in a grass bed during a four year study. The smallest crabs were virtually absent from the marsh creek and larger crabs that had molted three or more times were not observed until two to four weeks after settlement in the grass bed, again indicating migration out of grassbeds as the crabs grew larger.¹⁰⁵

Heck and Thoman⁴⁶ concluded that SAV beds in the lower Bay were important nursery habitats for blue crabs but those in the upper Bay (Eastern Bay) were not. These authors sampled with a trawl, however, and other workers have shown that trawls are very inefficient in comparison to push nets, crab scrapes,⁹¹ and drop nets combined with suction sampling.¹⁰⁵ In addition, a marked decline in vegetation occurred in the upper Bay during the study period and, finally, the area studied was too far up the Bay to be colonized by the smallest and most abundant juvenile crabs which use these habitats heavily in the lower Bay. Definitive studies of the relative importance of vegetated and unvegetated bottom as recruitment and nursery areas for the smallest blue crabs in Maryland waters have not been done.

In areas where the marsh is inundated by tidal water for substantial periods, the marsh surface can be an important habitat for blue crabs. Densities of blue crabs ranging from 1.3 to 22.1 m^{-2} were found in salt marsh, but only 0.6-5.6 m^{-2} on bare sand and mud bottoms. Where present, seagrass beds harbored the highest densities of crabs (2.8-50.6 m^{-2}). On average, crabs in the marsh were larger than those in the seagrass beds.¹³⁹

The value of eel grass beds as refuges from predation was shown in a New Jersey study. The authors found that tethered crabs were preyed upon at lower rates within eelgrass beds than in adjacent bare sand patches. Furthermore they reported that intermediate densities (around 500 g m^{-2} dry weight) of eelgrass provided better refuge from predation than either low or high eel grass densities. The authors thought that because the blue crab's main mode of predator avoidance is to bury in the substratum, high density eel grass provided less protection from predation because the dense root mass prevented burying behavior by the crabs. The dominant predators in this habitat were the American eel, oyster toadfish, other blue crabs, and probably the smooth dogfish. No effect of crab

size on the risk of predation was found in the range of 11-110 mm.¹⁵⁷

Sea lettuce provided more protection from predation than eelgrass beds during summer months but not in the fall.¹⁵⁸ Higher predation rates were found in saltmarsh creeks than in eelgrass beds, supporting the hypothesis of Orth and van Montfrans¹⁰⁷ that predation and lack of suitable refuge may contribute to lower juvenile crab abundance in marsh creeks as compared to eelgrass beds.

In contrast to earlier studies, investigations in 1986 and 1987 found no difference in density of juvenile crabs in eelgrass, sea lettuce, marsh creek, and adjacent unvegetated habitats in New Jersey. This lack of difference was attributed to the very low abundance (0-3 m^{-2}) of juvenile blue crabs during the study years. Densities of crabs were considerably higher in September, 1988 when mean numbers were 7.4 m^{-2} in eelgrass, 2.6 m^{-2} in unvegetated areas, and 3.6 m^{-2} in sea lettuce. Abundance of juveniles can vary greatly in space as well as time. At a site 28 km to the north, densities up to 40 m^{-2} were found in eelgrass beds in 1988.¹⁵⁹

There is evidence that eelgrass root mass and debris found in marsh creeks may provide protection from overwinter mortality of juvenile blue crabs. Juvenile crabs were found only in these habitats in March even though they were found in unvegetated habitats the previous November.¹⁵⁹

In lower Chesapeake Bay, molting activity is greater in seagrass beds than in marsh creeks. However, it is not known whether blue crabs actively seek grass beds for molting or if they simply stop there to molt when moving inshore from deeper water to molt. In the upper Chesapeake Bay, where no grass beds were present, crabs nearing ecdysis moved into a tidal marsh creek where molting occurred and migrated back to the river after molting.⁴⁸

There is evidence of differing habitat use by sex in blue crabs. The proportion of females in grassbeds was about 55%, but only about 37% of the crabs larger than 70 mm and only 19% of the smaller crabs in the marsh creek were females. Crabs in the grassbed were smaller than those in the marsh creek.¹¹⁵

Although seagrass beds have been found to be important nursery areas for juvenile blue crabs, estuaries in South Carolina, Delaware and southern New Jersey harbor substantial populations of blue crabs but are almost devoid of seagrasses.¹⁵⁹ In addition, it is interesting that although there was a wide-spread and major decline in the distribution and abundance of SAV species in the Bay from 1965 through 1980,¹⁰⁴ the decline in SAV was not reflected in the commercial landings of blue crabs during the same time.

There are no grass beds in the Rhode River near Annapolis and intermediate sized male crabs (80-120 mm) migrated into a tidal marsh creek to molt and moved back to the Rhode River after completing the molt. The sexes were unevenly distributed in this subestuary. At the river mouth, 54% of the crabs were males, whereas at the head of the river 65% were males, and in the tidal marsh creek 91% were males. The authors pointed out that because most of the crabs in the creek were in molt stages that did not eat, the creek provided a refuge from cannibalism during molting.⁴⁸

In another study at this site, crabs were fitted with ultrasonic transmitters that changed pulse rate when the crabs molted. The crabs selected shallow areas averaging 28 cm deep within a few meters of shore for molting. About equal numbers molted during the day and night. Most of the crabs molted downstream from the weir where they were captured, which contradicted the evidence gathered in the previous study that crabs molted upstream of the weir. All crabs did, however, remain in the creek to molt instead of moving into the shallows of the Rhode River.¹⁶¹

The adaptive significance of habitat selection by molting adult blue crabs was recently investigated in the Rhode River. This study found that pre- and post-molt males were more abundant in the tidal creek than in the river, whereas intermolt males and females approaching the terminal molt were more abundant in the river. No differences in molting success or increase in size were found between the two habitats. The authors concluded that mate availability was the main factor influencing habitat selection by the pubertal females and that tidal creeks provided a refuge from predation for molting male crabs.¹²³

SPECIAL PROBLEMS

Contaminants

The larval stages of crustaceans are generally more sensitive to toxic materials than the juvenile and adult stages. The sublethal effect most often seen in laboratory toxicity tests with blue crab larvae is a lengthening of the larval development period.^{32,33} Fortunately, blue crab larvae spend little time in the confines of the Bay where they would be most likely to be exposed to toxic substances. Juvenile and adult crabs may be exposed to toxic materials by burying in the sediment, by runoff from urban, suburban, and agricultural areas, and by eating contaminated food, especially bivalves.

Acute toxicity of a variety of chemicals to juvenile blue crabs has been determined at the U.S. Environmental Protection Agency Laboratory at Gulf Breeze, Florida. The information in Table 2 was extracted from a 1987 publication by that laboratory. Summaries of other toxicity studies are given below.

Petroleum hydrocarbons

Juvenile blue crabs were exposed to the water-soluble fraction of South Louisiana crude oil for 21 days. The crabs were very tolerant of the crude oil (LC_{50} was $4501 \mu\text{g/L}^{-1}$ on day 1 and declined to $3927 \mu\text{g/L}^{-1}$ on day 21). Sublethal effects included decreased energy intake and growth efficiency in inverse proportion to concentrations from 820 – $2504 \mu\text{g/L}^{-1}$.¹⁵⁰

Uptake of petroleum hydrocarbons by small blue crabs from water and food also has been studied.⁶⁶ About 10% of benzopyrene, methylcholanthrene, and fluorene dissolved in water was taken up by blue crabs after about two days. About 20-50% of ingested radiolabeled hydrocarbons was voided in feces. The crabs were able to metabolize the materials and the rate of elimination was rapid for the first three days after feeding. The tissues examined showed no tendency to retain hydrocarbons after transfer to clean water.

No differences in resistance of blue crabs to naphthalene at salinities of 10 or 30 ppt were found.¹¹⁶ Adult intermolt crabs were exposed to water-soluble naphthalene at 0, 37.5, and 75% of the 24 h TLm in a flow through system. The 24 h and 48 h TLm values were 2.4 and 2.3 mg/L^{-1} , respectively. At the lower salinity, crabs responded to both concentrations with increased ventilation and at the higher concentration, suffered increased tissue hydration. At the higher salinity, crabs increased gill ventilation and perfusion while experiencing dose-dependent hemolymph alkalosis.

Juvenile crabs exposed to daily doses of 1 mg/L^{-1} benzene in a static system had longer intermolt cycles, slower rates of limb regeneration, and reduced growth increments at ecdysis. Actual concentrations in the static chambers fell to about 0.3 mg/L^{-1} after 6 h and stabilized at that level.¹⁴

Polynuclear aromatic hydrocarbons

Tissue burdens of lipophilic polycyclic aromatic hydrocarbons (PAH) of blue crabs from the southern portion of Chesapeake Bay were studied by Hale.⁴⁰ Body burdens were highest in hepatopancreas and least in muscle tissue, while ovarian tissue was intermediate. Alkylated PAH, abundant in petroleum, predominated among the 76 compounds identified. This is in contrast to the situation in bivalve mollusks and sediments of Chesapeake Bay in which unsubstituted PAH predominated. Crabs collected from the lower James river in 1981 carried the highest burdens (median concentration $310 \mu\text{g kg}^{-1}$) followed by those from the upper Rappahannock at $200 \mu\text{g kg}^{-1}$, Pocomoke Sound at $28 \mu\text{g kg}^{-1}$, and the mid-James at $9.3 \mu\text{g kg}^{-1}$. In the laboratory, accumulation of benzo(a)pyrene from a solution of 0.3 mg/L^{-1} was rapid and depuration was efficient but occurred at a slower rate.⁴⁰

Hale also reported burdens ranging from 400 to 9,820 $\mu\text{g kg}^{-1}$ of chromatographically unresolvable complex mixtures in 39% of the hepatopancreas samples.

Polychlorinated biphenyls

Researchers in South Carolina found up to 0.86 mg kg^{-1} of polychlorinated biphenyls (PCB) in muscle tissue of adult blue crabs taken at the outfall of a waste water treatment facility. The tissue burden was about equally divided between 1248 and 1254. Much lower concentrations were found in crabs captured only a few hundred meters away.⁸⁴ Maximum levels of 0.08 mg kg^{-1} were reported for crabs from Maryland waters.³¹ Blue crabs are known to bioaccumulate PCB from water and sediment.¹⁰⁰ Other workers have found the highest concentrations of contaminants in hepatopancreas samples as opposed to other tissues.⁸⁹ A maximum concentration of 130 $\mu\text{g kg}^{-1}$ of PCB was found in the hepatopancreas of adult female crabs from a mid-James River station.⁴⁰

Kepone

Kepone residues in crabs from the James River were as high as 0.81 $\mu\text{g g}^{-1}$ and coincided with a 90% decrease in commercial landings of crabs from 1972 through 1975. Average kepone concentrations in typical blue crab prey items from the James ranged from 0.09 to 2.0 $\mu\text{g g}^{-1}$. A moratorium on the harvest of crabs from the James River was in effect in 1976.¹²⁰ The plant that manufactured kepone was closed in July, 1975, by order of the Virginia Health Department.¹² Kepone is very stable, and remains a problem because contaminated sediments can be resuspended by dredging,⁸⁰ by storms, and possibly by bioturbation.

In laboratory studies, 1.0 $\mu\text{g L}^{-1}$ of kepone was acutely toxic to blue crab larvae. Sublethal effects on development time to the first crab stage were detected at 0.1, 0.5 and 0.75 $\mu\text{g L}^{-1}$ kepone.^{11,12}

Kepone in water appears to be relatively non-toxic to adult crabs (96-h $\text{LC}_{50} > 210 \mu\text{g L}^{-1}$).¹¹⁹ Data on toxicity of food containing kepone to juvenile blue crabs is conflicting. Greater mortality occurred in juvenile crabs fed oysters containing 1.9 $\mu\text{g g}^{-1}$ kepone twice a week than in control crabs, but significant mortality was not detected in crabs fed oysters containing 0.15 $\mu\text{g g}^{-1}$ kepone. Signs of poisoning included excitability, followed by lethargy, convulsions and death.¹²⁰ In contrast, another study reported no significant mortality after 65 days in juvenile blue crabs fed striped bass and oysters containing kepone at 2.5 and 2.26 $\mu\text{g g}^{-1}$, respectively. Reasons for the different findings in these two studies may include different water temperatures, pulsed feeding as opposed to daily feeding, and higher dose in the first study because of smaller crab size.³⁷ The latter study did report sublethal effects of kepone ingestion at levels found in food organisms in the James River. These effects included in-

creased respiration, excitability, and decreased ability to locate and manipulate food. The authors postulated that these effects could result in increased mortality at the molt, in crabs molting in hypoxic waters, because of higher oxygen demand during the molt and increased mortality from predation due to the behavioral abnormalities found. Significant reductions in molting rate were found in juvenile blue crabs fed oysters from the James River that contained 0.15 $\mu\text{g g}^{-1}$ kepone. Control crabs molted an average of 1.4 times in 56 days whereas those fed contaminated oysters only molted an average of 0.48 times.¹²⁰

Uptake of kepone in muscle of juvenile blue crabs fed oysters contaminated at 0.15 $\mu\text{g g}^{-1}$ and 0.25 $\mu\text{g g}^{-1}$ was rapid and no sign of depuration could be detected during a 28 day period following exposure. Some loss of kepone was evident beyond 28 days but the compound still was detectable in crabs held for 90 days in a kepone-free environment.¹²⁰

Mirex

Mirex is an organochlorine insecticide that is chemically similar to kepone and is used in baits to control fire ants. Mirex was toxic to blue crab larvae at 1.0 and 10.0 $\mu\text{g L}^{-1}$ after 5 days of exposure. Concentrations of 0.01 and 0.1 $\mu\text{g L}^{-1}$ had no effect on the duration of development of blue crab larvae from hatching to the first crab stage.⁸ Juvenile blue crabs were poisoned by mirex bait but adult and subadult (76-127 mm carapace width) crabs were not affected by ten times the U.S. Department of Agriculture's suggested application rate.⁷⁸ Mirex leached from fire ant bait was toxic to blue crabs at concentrations below 0.53 $\mu\text{g L}^{-1}$ during a 28 day continuous exposure. It was most toxic at high water temperatures typical of summer and the earliest deaths occurred at six days. Blue crabs concentrated mirex by 2,300 times over a 28 day period.¹³⁸ Mirex was absorbed through the gills and was concentrated in the hepatopancreas. Exposure to solutions of 0.22 $\mu\text{g L}^{-1}$ mirex for 15 minutes to 16 hours resulted in accumulations of 1.6-31 $\mu\text{g g}^{-1}$ of mirex in the hepatopancreas and 0.65 to 1.1 $\mu\text{g g}^{-1}$ in muscle. Crabs responded to the exposures by progressing from increased aggressiveness to decreased aggressiveness to loss of equilibrium and death, although a few recovered.¹²¹

Malathion

Some blue crab larvae could complete development through the 46 - 52 day larval period in concentrations of malathion ranging from 0.02 to 0.11 mg L^{-1} . However, sublethal effects on development time and mortality were noted at all concentrations used. Blue crab larvae were most sensitive to this organophosphate insecticide in the early stages of development (zoal stages I-III), whereas the megalopal stage was not sensitive to malathion at these concentrations.⁹ Blue crab larvae were less sensitive to malathion than larvae of a mud crab, whereas the

opposite was true of larvae exposed to the chlorinated hydrocarbon methoxychlor.¹⁰

DDT

Juvenile blue crabs were unaffected by a nine-month exposure to 0.0003 mgL⁻¹ DDT, but at 0.005 mgL⁻¹ they exhibited irritability and paralysis after a few days, and at concentrations greater than 0.005 mgL⁻¹ they could only survive a few days.⁷⁷ In a field study, blue crabs were found living in a Florida marsh area that was contaminated with DDT. The hepatopancreas and muscle tissue of these crabs contained total DDT-R residues of 39.0 and 1.43 mg kg⁻¹. No field mortality was noted in the contaminated area until winter when the water temperature dropped.⁶¹

Chlorine, chlorine-produced oxidants, and other halogenated compounds

Kaumeyer and Setzler-Hamilton⁵⁷ cited three studies on the effects of halogenated compounds on adult blue crabs in their Table 7. The 48-h LC₅₀ for total residual chlorine (TRC) at 25°C and 10 ppt was given as 0.75 mgL⁻¹ from a study by Vreenegoor *et al.* 1977. In another citation given as "Public Service E & G Co. 1978" an EC₅₀ avoidance at 0.20 mgL⁻¹ was given for TRC. Walker *et al.*, 1979 reported an LC₅₀ of 16.0 mgL⁻¹ for CPTH (3-chloro-4-methyl-benzamine hydrochloride). These references were not found in the bibliography given by Kaumeyer and Setzler-Hamilton.

The 96-hr LC₅₀ for blue crabs exposed to chlorinated sea water at 21°C and 14 ppt was 0.84 mg Cl₂ L⁻¹ from chlorine-produced oxidants (CPO). Mortality was uncommon at exposures below 0.61 mgL⁻¹ but reached 100% with exposures of 1.15 mgL⁻¹. Decreased oxygen consumption was measured after a two hour exposure to 0.79 mgL⁻¹, but was apparently a temporary effect as no consistent changes in oxygen consumption were found in 96-h exposures to 0.99 mgL⁻¹ CPO. Changes in the ventilation rates of crabs were noted at the short term exposures but not in the long term exposures. No observable damage to gill tissues were seen in histological preparations of gills.⁶³

Exposures to CPO at 0.36 to 1.04 mgL⁻¹ did not affect serum constituents except for magnesium. Regulation of this ion in the serum was disrupted during 96-hr exposures of crabs to 0.47 mgL⁻¹ CPO and higher. The author hypothesized that increased serum magnesium levels interfered with neural activity and may have caused death.⁶³

He also noted that blue crabs were tolerant of chlorinated sea water at concentrations only rarely expected in the environment near outfalls. In addition, crabs could detect low levels of chlorinated sea water and would probably avoid concentrations that might cause sublethal effects.⁶³

Heavy metals

Effects of cadmium nitrate on survival and larval development of blue crabs have been found. Exposure to concentrations of 0.05 and 0.15 mgL⁻¹ for 240 hours caused a 50% increase in the development period at all salinities tested (10, 20, and 30 ppt). At the lowest test concentration (0.05 mgL⁻¹), mortality was negligible at 30 ppt salinity; 15% greater than controls at 20 ppt; and 47% greater than controls at 10 ppt. Exposure to 0.15 mgL⁻¹ CdNO₃ resulted in mortalities 32-57% greater than controls at all three salinities. At the highest concentration (0.25 mgL⁻¹), all larvae died at all salinities.¹¹³ It should be noted, however, that a salinity of 10 ppt is lethal to blue crab larvae and 20 ppt is stressful.

Effects of cadmium on juvenile crabs were determined at 21 °C. Reported 48-h LC₅₀ was 0.9, 9.4, and 23.8 mgL⁻¹ for crabs exposed at salinities of 1.0, 15.0 and 35 ppt, respectively. Concentrations for 96-h LC₅₀ were roughly one-half of the 48-h values.³⁸

Adult blue crabs acclimated to various salinities were highly tolerant of cadmium in the water. Exposure to 11.14 µgL⁻¹ cadmium was lethal within eight days but exposure to 0.11 µgL⁻¹ and lower concentrations had no effect and cadmium did not accumulate in tissues. After a 27 day exposure to 0.2 µgL⁻¹ cadmium, only the gills, hepatopancreas and carapace had cadmium concentrations higher than the controls.⁵²

Acute toxicity of chromium (as potassium dichromate) to juvenile blue crabs was determined at 21°C and at salinities of 1.0, 15.0 and 35 ppt. The reported 48-h LC₅₀ for the three salinities were: 39.0, 126.0, and 130.0 mgL⁻¹.³⁸

A 96-h LC₅₀ of 4.6 mgL⁻¹ for selenium (as sodium selenite) was reported for juvenile blue crabs at 22°C and 30 ppt¹⁵¹, cited in 57

Exposure to 10 µgL⁻¹ mercury significantly increased mortality of megalopae developing in 10 ppt seawater but did not effect megalopae at salinities between 20 and 40 ppt. At 20 µgL⁻¹ mercury, survival through metamorphosis was reduced at all salinities. Development time of megalopae was prolonged by exposure to mercury. The first and second juvenile crab stages were not affected by exposure to mercury at these concentrations.⁸⁷

In a recent review of the effects of temperature and salinity on the toxicity of heavy metals to marine and estuarine invertebrates, no studies of toxicity of arsenic, copper, lead, mercury, nickel, or zinc to blue crabs were cited.⁸⁸

Overharvest

As mentioned previously, there is concern that increased fishing pressure may become detrimental to the blue crab population. However, the record of commercial landings

does not indicate a decline in abundance of blue crabs to date.

Diseases

Diseases, parasites and commensals of blue crabs were reviewed by Millikin and Williams.⁹² Although a variety of diseases caused by viral, bacterial, and protozoan agents are known, their importance to natural populations has not been established. Many of the known diseases do become problems under the specialized conditions found in crab shedding operations.

Two organisms that reduce the number of eggs hatched in natural populations of blue crabs are a marine fungus (*Lagenidium callinectes*) and a nemertean worm (*Carcinonemertes carcinophila*). The fungus may be very prevalent in some years and localities and may destroy more than 24% of an egg mass. The worms live in the gill cavity of adult female crabs and migrate to the egg mass after it is extruded. Although the worms may consume large numbers of eggs, the impact on the population of blue crabs is undetermined.⁹²

Boat interference

No studies on the effects of boats on blue crab populations were found in the literature. However, pollution from marinas, bottom paint, toxic leachates from dock pilings and bulkheads and mechanical factors such as substrate disturbance and direct contacts, all must affect the crab population to some extent.

Shoreline development

Because shallow near-shore habitats are important molting and foraging areas for blue crabs, shoreline development may be a major threat to blue crabs. The natural land-water interface can be destroyed by bulkheading and near-shore habitats are especially vulnerable to degradation from pollutants in urban, suburban and agricultural runoff, to disturbance by boat wakes, and to other man induced changes.

Power plants

Abbe¹ concluded that the Calvert Cliffs nuclear power plant had no effect on the population of crabs in the area. He also summarized reports on impingement studies at this and other plants, and noted that although millions of crabs are caught on the plant screens each year, impingement and subsequent wash-off from the screens had virtually no effect on survival of crabs.

RECOMMENDATIONS

Habitat

Reduce the area of bottom covered by hypoxic water during the summer months. A DO > 3 mgL⁻¹ at 25-28°C should be safe for blue crabs. Maintaining DO at or above

this concentration should provide more foraging and living space for crabs.

Preserve marsh-to-shallows interfaces and control runoff of contaminants by limiting the effects of shoreline development. These nearshore areas are critical for feeding and molting.

Preserve existing SAV beds and restore beds that have deteriorated. Sea grass beds are critical nursery and molting habitats.

Reduce toxic inputs. Because bivalves (which bioaccumulate toxics) are the most important component of the diet of blue crabs, crabs are susceptible to poisoning through contaminated food.

Monitoring

Monitor the population level of juvenile crabs using fishery independent methods. Declines in abundance of juveniles may indicate that harvest restrictions should be implemented.

Research

Better data are needed on habitat use by size class, season, and locality within the Bay. Sea grass beds are important habitats in the lower Bay, but are much less abundant north of Smith Island. Most of the upper Bay bottom is unvegetated. We know little about the importance of different substrate types and depths in areas where SAV beds are absent. Trawls and dredges do not sample different substrate types with equal efficiency and therefore cannot provide realistic data on the relative importance of different bottom types. The use of drop-nets combined with suction sampling appears to be the method of choice for this work.

Better information on fishing mortality (commercial and recreational), natural mortality, age structure of the population, growth, catch effort, and population size is needed for management of the fishery.

CONCLUSION

The blue crab is an amazingly adaptable creature which can, and does, inhabit virtually all habitats within the Chesapeake Bay. Except for deep hypoxic waters in the summer and shallow habitats lost to development, blue crabs utilize all of the Bay. The largest identifiable threats to the blue crab are increasing fishing pressure and shoreline development. But, because the blue crab is so important in food webs, both as prey and predator, changes in populations of its primary food items, major competitors, or predators could have important effects on the population of blue crabs.

The annual harvest of blue crabs is subject to major variations. No clear relationship of harvest to major changes within the Bay are evident (such as increased areas of low dissolved oxygen, winter kill during severe winters, tropical storm Agnes in June of 1972, or the Baywide decline in SAV during the period from 1965-1980). It is important to emphasize, however, that effects of perturbations are difficult to detect because the simple landing statistics do not provide information on changes in effort required to land a given number of crabs or provide real measures of the population size of crabs and the proportion of the population that is harvested. Because larvae are dispersed to continental shelf waters to develop, fortuitous meteorological conditions during the time of planktonic existence can have major effects on the number of post-larvae that reinvade the estuary. Since we have no control over such events, the best that we can do is to insure that suitable habitat exists for crabs each year, including important shoreline and seagrass habitats.

Reduction of the area covered by hypoxic water in the summer and an increase in the area occupied by SAV would increase habitat available to blue crabs and their prey. Protecting existing shallow shoreline habitats from development (such as bulkheading), from dredging, and from runoff of urban, suburban, and agricultural pollutants, may be even more important in maintaining the stock of Chesapeake Bay blue crabs. These shallow near-shore habitats are important for molting and foraging. The extent of these areas is enormous, given the 5000 mile shoreline of the Bay, and is likely a very important factor in the production of the large annual yield of blue crabs from the Chesapeake.

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Table 1. Major foods of Blue Crabs

Reference	23 ^a	133 ^a	64 ^b	2 ^c
Food Class	Percent of diet			
bivalves	34-63	39	40.4	42
crabs and other crust.	10-36	15	28.6	21
fishes	5.4	19.4	11.9	26
annelids		1.8	0.46	5
plant matter	12	3.9	4.0	29 ^d 25 ^e
detritus	19-27	19.8	7.4	

a. % by volume

d. algae

b. % by weight

e. vascular plants

c. % of stomachs containing the item

Table 2. Toxicity to Blue Crabs^a

CHEMICAL	TEMPERATURE °C	SALINITY ppt	DURATION h	FLOW ^b	TEST	CONCENTRATION
aldrin (insecticide)	28	21	48	FT	EC ₅₀	23 µg/L ^{-1 c}
antimycin A (piscicide)	25	29	48	FT	EC ₅₀	>100 µg/L ^{-1 c}
azinphos-Methyl (insecticide)	27	27	48	FT	EC ₅₀	320 µg/L ^{-1 c}
carbaryl (insecticide)	30	28	48	FT	EC ₅₀	320 µg/L ^{-1 c}
chlordane (insecticide)	29	23	48	FT	EC ₅₀	260 µg/L ^{-1 c}
chlordecone (Kepone) (insecticide)	19	20	96	FT	LC ₅₀	>210 µg/L ^{-1 d}
chlorpyrifos (insecticide)	17	20	48	FT	EC ₅₀	5.2 µg/L ^{-1 c}
2,4-D Propylene Gl Butyl Ether Ester (herbicide)	24	29	48	S	EC ₅₀	2,800 µg/L ^{-1 c}
dieldrin (insecticide)	18	26	48	FT	EC ₅₀	240 µg/L ^{-1 c}
endosulfan (insecticide)	30	24	48	FT	EC ₅₀	19 µg/L ^{-1 c}
endrin (insecticide)	11	16	48	FT	EC ₅₀	15 µg/L ^{-1 c}
fenthion (insecticide)	28	25	48	FT	EC ₅₀	2.3 µg/L ^{-1 c}
heptachlor (insecticide)	17	27	48	FT	EC ₅₀	68 µg/L ^{-1 c}
malathion (insecticide)	30	25	48	FT	EC ₅₀	>1000 µg/L ^{-1 c}
methoxychlor (insecticide)	31	27	48	FT	EC ₅₀	320 µg/L ^{-1 c}
mirex (insecticide)	31	24	48	FT	EC ₅₀	>2000 µg/L ^{-1 c}
naled (insecticide)	28	25	48	FT	EC ₅₀	220 µg/L ^{-1 c}
ozone (water sterilant)	25	7.4	96	S	LC ₅₀	0.26 mg/L ^{-1 d}
toxaphene (insecticide)	19	27	48	FT	EC ₅₀	180 µg/L ^{-1 c}

^aMayer, F.L., Jr. 1987. Acute Toxicity Handbook of Chemicals to Estuarine Organisms. U.S.Environmental Protection Agency. April 1987.^bFT = Flow through;

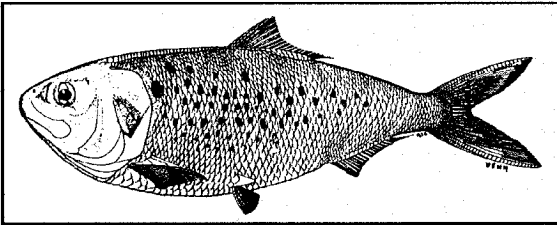
S = Static

^cNominal concentration^dMeasured concentration

ATLANTIC MENHADEN

Brevoortia tyrannus

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The Atlantic menhaden is one of the most abundant species in estuarine and coastal Atlantic waters. The second most important species harvested in the United States in terms of quantity, it is processed for its oil, protein meal and solubles, and is used exclusively as bait for commercial and recreational fishing. Menhaden are consumers of phytoplankton and plant detritus and, in turn, are fed upon by many predatory fish and birds.

The Atlantic menhaden is a member of the herring family, but unlike most herrings and shads, the menhaden is a coastal ocean spawner. It ranges from Nova Scotia in Canada to central Florida. The Chesapeake Bay is an important nursery ground for immature menhaden. The critical early stages are spent in coastal waters and, consequently, the eggs and larvae are not exposed to pollutants in the Bay. The Atlantic menhaden stock has remained relatively stable in recent years. Menhaden are able to tolerate sudden shifts in salinity and are found throughout the Bay from almost freshwater to high salinity.

The menhaden stock must be managed wisely if it is to withstand heavy fishing pressure and maintain its vital ecological roles as an important converter of phytoplankton and plant detritus and as an important food source for many other species.

INTRODUCTION

The Atlantic menhaden is one of the most abundant fish in the coastal and estuarine waters of the mid-Atlantic. During summer months in the Chesapeake Bay this herring-like fish swarms in large schools; acres of these silvery fish are frequently seen dappling the water's surface. Watermen use menhaden for crab bait, recreational fishermen grind them and spread their oily residue, called chum, to attract gamefish, and commercial fishermen harvest menhaden in enormous quantities. Menhaden are food for many fish species, especially bluefish and striped bass, and for birds such as herons, egrets, ospreys and eagles.

Approximately two billion pounds of Atlantic and Gulf menhaden were caught in 1989 making these the second most important fishery species in the United States in terms of quantity harvested. Menhaden are not used di-

rectly as human food, but are processed primarily for industrial uses such as fish oils and meal for livestock feed.

Although many Chesapeake Bay anadromous and resident fish species have declined, stocks of oceanic species such as Atlantic menhaden have remained relatively stable in recent years.¹⁹ Menhaden landings have increased since the early 1970's. Landings peaked at 418,000 metric tons in 1983. Landings in 1989 were approximately 322,000 metric tons. Biological investigations of menhaden stocks indicate relatively stable populations in recent years. Fluctuations in landings the past few years are generally not a reflection of stock strengths but, rather, are indications of complex national and international market conditions. The Chesapeake Bay area clearly dominates Atlantic coast landings. Menhaden are harvested in Virginia's portion of the Chesapeake Bay principally by purse seine vessels and pound nets. Maryland prohibits purse seining in its sector of the Bay where menhaden are chiefly caught in pound nets. Research on

ATLANTIC MENHADEN

menhaden is conducted principally at the National Marine Fisheries Service Laboratory in Beaufort, North Carolina. Menhaden stocks are managed through the joint efforts of the Atlantic States Marine Fisheries Commission, individual states, the fishing industry, and the National Marine Fisheries Service.

BACKGROUND

The preferred common name is Atlantic menhaden; other common names are pogey, moss-bunker, bunker, fat-back, shad, alewife and hugmouth. Menhaden are part of the family Clupeidae, which includes the closely related herrings and shads. Most members of this group are anadromous in that they migrate to freshwaters to spawn. Menhaden, however, spawn in coastal ocean waters and are considered catadromous spawners, which means that they develop in the less saline waters of the Bay and return to the ocean to spawn.

Morphology

The adult Atlantic menhaden is elongated and laterally compressed. The snout is blunt with a prominent median notch; the tip of the lower jaw projects beyond the upper. The dorsal fin is small; elevated anteriorly, and inserted about midway between the tip of the snout and the caudal base. The origin of the anal fin is under or just behind the tip of the last dorsal ray. The pectoral fin is slightly falcate and is inserted low on the body; the lower lobe of the tail is slightly longer than the upper.

Atlantic menhaden are blue, blue-green, or blue-brown above. The sides and fins are silvery with a strong yellow or brassy luster. They have a dark round or vertically elongated shoulder spot followed by a number of smaller spots arranged in somewhat horizontal rows. The peritoneum is black.¹⁵

One-year old fish are approximately 135 mm in length (5.5 in); two-year olds, 215 mm (8.5 in); three-year olds, 250 mm (10 in); five-year olds, 270 mm (11 in); and five to seven-year olds, 300-350 mm (12-15 in). These measurements are fork length, i.e., from the tip of the snout to the fork of the tail. The longest menhaden on record is an eight-year old, 418 mm (16 in) fish that weighed over three pounds. Menhaden generally weigh between 2-3 ounces at one year to about one pound at six years and older.³²

Geographic range

The Atlantic menhaden is indigenous to the coastal waters and estuaries of the eastern United States and Canada, ranging from Nova Scotia to central Florida.²⁷

The Chesapeake Bay is an important nursery for juvenile menhaden; they occupy almost the entire Bay and its tributaries from above Baltimore to the mouth of the Bay in Virginia. Larval menhaden enter the Bay in early sum-

mer and move into lower salinity waters in estuarine tributaries where they are found in great abundance. They then metamorphose into juveniles at a length of about 34 mm.^{23,38} Throughout summer, one and two-year old immature fish are found in large concentrations. Juvenile menhaden remain in the Bay until fall when most migrate from the tributaries and the Bay into the ocean. They then migrate southward and winter offshore south of Cape Hatteras. The following spring they migrate northward as adults to the Chesapeake Bay area and into New England waters.¹⁰

LIFE HISTORY

Atlantic menhaden mature sexually at about two years; fish of the same age are progressively larger toward the northern portion of their range, although they are sexually mature at smaller sizes in more southern areas.³⁴ Fish in the South Atlantic Bight mature at a minimum fork length of 180 mm, whereas those in the Middle Atlantic Bight are sexually mature at a minimum of 210 mm fork length.²⁸

Atlantic menhaden spawn in inshore waters over most of the continental shelf, as well as in bays and sounds from Long Island waters northward.^{1,33} Reintjes³¹ reported menhaden eggs and small larvae at the mouth of the Chesapeake Bay, but suggested that spawning in the Bay was minor in comparison to total population numbers.

Atlantic menhaden spawn during the entire year, at one location or another.¹ Several studies indicate that menhaden spawn in waters north of Long Island from May to September, in the Mid-Atlantic Bight south of Long Island from March through May and again in September and October, and south of Cape Hatteras from October through March.^{16,18,31}

Atlantic menhaden eggs are buoyant, spherical, and highly transparent; they normally hatch in about two days at 15-20°C.¹⁵ The larvae are pelagic and probably spend about one month in waters over the continental shelf before entering Chesapeake Bay at approximately 10 mm or larger.^{24,26}

ECOLOGICAL ROLE

Atlantic menhaden begin feeding on zooplankton about four days after hatching.³³ They are size-selective plankton feeders and, although there is no direct evidence of the food they ingest before entering the estuary, it is quite possible that they feed on pteropods and bivalve larval stages, as well as crustacean nauplii which are food sources for other members of the herring family.

As post-larval menhaden metamorphose into prejuveniles (approximately 30 mm) they develop a functional branchial filtering apparatus which enhances their ability

to graze on phytoplankton and suspended detritus. Late-stage juveniles and adults are primarily herbivores, but they also retain the ability to feed on zooplankton.⁵

Menhaden are an adaptable species and are capable of grazing on several species of benthic diatoms as well as organic detritus.^{14,17} Recent evidence suggests that juvenile Atlantic menhaden readily digest cellulose and other vascular plant material, and that detritus of vascular plant origin forms an important component of their diet.²² McHugh²⁵ calculated that an average size adult menhaden could filter about 3.9 gallons (15.2 L) of water per minute. Assuming a steady filtering rate over a six-month period, an individual fish could therefore filter the plankton from somewhat more than a million gallons (3.9×10^6 L) of water in 180 days.

Larval and juvenile menhaden are seasonally very important components of estuarine fish assemblages.^{2,29,36} Given the tremendous numbers, individual growth rates, filtering and feeding capacity, and seasonal movements of these fish, they consume and redistribute significant amounts of energy and materials on an annual basis, both within and between estuarine and continental shelf waters.

Atlantic menhaden are fed upon by many predatory fish species both in coastal ocean waters and the Chesapeake Bay. Their habit of forming large schools attracts voracious feeders such as striped bass, bluefish, Spanish mackerel, tuna, and sandbar sharks. In addition, herons, egrets, ospreys, and eagles also prey on the Atlantic menhaden.

HABITAT REQUIREMENTS

Because Atlantic menhaden spawn in marine waters and move into the Bay as pelagic larvae at approximately one to two months old, their sensitive egg and early larval life stages are not exposed to habitat conditions in the Bay. As a result, contaminants and other associated water quality problems do not appear to have caused a discernible decline of Atlantic menhaden in the Chesapeake Bay. It is important, however, to identify known adverse conditions that could affect the health of the stock and jeopardize the management of this important ecological and commercial species.

Water quality

Although information on water quality is generally inadequate to assess the effects of pollution on marine fish stocks, lack of evidence of a direct effect is no cause for optimism.³⁵ Some marine species may be severely affected, but we are unable to distinguish pollution effects from overfishing, predation, or environmental causes.³⁷ Research on Atlantic menhaden has focused primarily on early development, life history and growth, population

structure, movements, the impacts of fishing on age structure and abundance, and the development of statistical methods to predict changes in abundance. Studies specific to menhaden temperature, salinity and oxygen requirements are discussed below.

Temperature

Studies correlating survival response of larval Atlantic menhaden to experimental temperatures involved acclimating larvae to various temperatures and then subjecting them to experimentally altered temperatures that they might encounter in their environment. The relationships between survival time and temperature were then determined.^{13,20} Other studies on the effects of thermal effluents on juvenile Atlantic menhaden concluded that rapid mortality occurred in effluents of greater than 33°C.^{21,39}

Salinity

Menhaden can withstand substantial variations in salinity ranging from almost freshwater (3.5 ppt) to full strength ocean salinity.^{6,32} Juvenile Atlantic menhaden can tolerate sudden salinity shifts,⁶ which may account for the distribution of this species throughout the Bay. Hettler¹¹ reported that juvenile menhaden grew faster in low salinity water (5-10 ppt) than in higher salinities (28-34 ppt). Juvenile menhaden are often very abundant in the low salinity waters of mid- and upper tributaries, as well as in the mainstem of the upper Bay. Some of these areas frequently suffer from poor water quality.

Dissolved oxygen

Atlantic menhaden often suffer mass mortalities during summer months, generally in small coves and heads of creeks. The teeming numbers of fish milling about in the warm shallow waters may literally exhaust the dissolved oxygen, (DO) resulting in the deaths of hundreds to thousands of fish.³³ Algal and bacterial respiration associated with active or decaying blooms probably contribute to DO depletion and mass mortalities of menhaden. Dissolved oxygen tolerance studies indicated that significant mortalities occurred at a concentration of 1.1 mgL⁻¹ DO when the fish were acclimated at 28°C.³

Structural habitat

There is little information on habitat structure with respect to Atlantic menhaden. This species lives throughout the Bay and its tributaries from the high salinity zones to freshwater. The young are often found in shallow water areas, but they commonly occur in the open, deeper waters of the Bay.

SPECIAL PROBLEMS

Harvest

Atlantic menhaden is a heavily fished species along the Atlantic coast. Demand is tied closely to world markets for

soybean oil and related products. The menhaden industry is a serious competitor with the soybean industry. When the demand for menhaden products is high, due possibly to fluctuations in soybean prices or availability, heightened harvesting pressure is placed on the menhaden stock. It is imperative that stock assessments and fishery management decisions be made on a timely basis to conserve the stock strength at an acceptable level.

Heavy fishing along the Virginia and North Carolina coast on the zero year class, often called "peanuts," as they migrate out of the Chesapeake Bay is of concern to some biologists and fisheries managers. These fish are not sexually mature; they will never have an opportunity to spawn and because of their small size their oil content is individually quite low.

Maintaining a viable and competitive industry is one concern. Equally important is maintaining a healthy stock of menhaden which convert energy derived from Bay plankton and vascular plant detritus to thousands of tons of fish. Menhaden is of paramount importance as a food fish for many other species in the Bay and in the ocean. The ecological role of menhaden in the Bay and coastal ocean cannot be overstated. It is extremely important that the stock be maintained and managed wisely.

Contaminants

Limited toxicity information is available for menhaden larvae. Except for the studies of tributyltin (TBT) toxicity reported below, virtually all toxicity tests have been related to the effects of chlorine, alternative disinfectants (bromine, ozone), and dechlorination agents. Larvae have been exposed experimentally to free residual chlorine with no mortality demonstrated at a concentration of 0.3 mgL^{-1} . A reduction in survival, however, did occur at 0.5 mgL^{-1} at all exposure times greater than three minutes.¹²

Studies on juvenile menhaden exposed to total residual chlorine suggest that chlorine-produced oxidants elicit a threshold response rather than a gradient response.^{7,30}

The toxicity of TBT to juvenile Atlantic menhaden was evaluated in an acute toxicity study, an avoidance study, and a sub-chronic toxicity study.^{4,8,9} Juvenile menhaden were able to avoid concentrations of $15 \text{ } \mu\text{gL}^{-1}$. Juveniles exposed to concentrations of 0.093 and $0.490 \text{ } \mu\text{gL}^{-1}$ of TBT

for 28 days had 100% survival rates. Histological examinations of juveniles after TBT exposures did not demonstrate any absolute effects due to variations between individuals.⁹

CONCLUSIONS

The Atlantic menhaden is an abundant member of the herring family that is harvested for its oil- and protein-rich flesh. Purse seine fishing for menhaden takes place along the Atlantic coast and in the Virginia half of the Chesapeake Bay. Menhaden are caught in pound nets in Maryland's portion of the Bay.

Atlantic menhaden spawn in Atlantic coastal waters and enter the Chesapeake Bay as larvae where they remain for about a year feeding on plankters and plant detritus. They are an important prey species and are avidly fed upon by bluefish and striped bass. Menhaden migrate from the Bay in late summer and fall at approximately one-year old and move southward along the coast where they are subject to heavy fishing pressure. There is some concern on the part of biologists and resource managers that menhaden should be allowed to mature and spawn (two-years old) before they are harvested.

Few studies have been done on water quality and habitat requirements concerning the Atlantic menhaden. Their most vulnerable life stages are spent in the comparatively clean coastal waters of the Atlantic Ocean. The productive waters of the Chesapeake Bay serve as a grow-out nursery for the young fish at a stage when they are less sensitive to pollutants.

The Atlantic menhaden is a commercially valuable and an ecologically critical species which must be carefully managed along the Atlantic coast and in estuaries such as the Chesapeake Bay. Fishing pressure must be closely monitored and the necessary steps taken to maintain a healthy spawning stock if it is to support a major commercial fishing industry and serve as a key food source for such important species as bluefish and striped bass.

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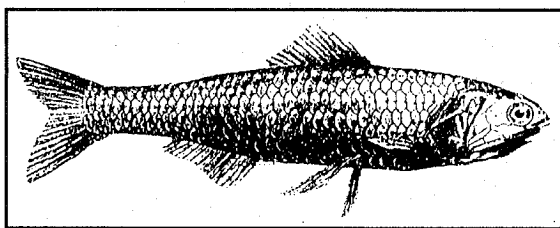
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BAY ANCHOVY

Anchoa mitchilli

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The bay anchovy, a small, schooling species, is the most abundant fish in Chesapeake Bay. It is a major consumer of plankton and is itself a major food of predatory fish, making it a key species in the Bay's food web. The bay anchovy occurs throughout the Bay and is widely tolerant of salinity and temperature. It lives to three years of age, seldom grows longer than 90 mm, and spawns in late spring and summer when low dissolved oxygen (DO)

may limit the distribution of all life stages. Oxygen levels below 3.0 mgL⁻¹ can be lethal to eggs and larvae and DO below 2.0 mgL⁻¹ is critical. Specific habitat features, structure, and shoreline development are not of particular concern for bay anchovy, but hydrographic features that affect water quality could limit its distribution and abundance. Surprisingly little is known about toxicant effects on bay anchovy. Bay anchovy losses from being entrained and impinged in power plant cooling systems may affect its abundance as well as that of fishes that consume it.

Bay anchovy populations in the Chesapeake Bay fluctuate annually, but no long-term declines have occurred. Deteriorating water quality in the future could affect its reproductive potential. Summer hypoxia already potentially limits its distribution and productivity in the Maryland portion of Chesapeake Bay. A better knowledge of toxicant effects on all life stages and better definition of the bay anchovy's key role in food webs will be important to define water quality criteria that may be critical.

INTRODUCTION

The bay anchovy is the most abundant fish in the Chesapeake Bay. This small, unexploited species is widely distributed along the Atlantic coast of the United States where it plays a key role in estuarine and coastal food webs. It is a schooling species that is a major consumer of plankton and is itself a major prey of large predatory fish, including bluefish, striped bass, and weakfish. Bay anchovy abundance has fluctuated significantly in Chesapeake Bay in recent years, but there is no evidence of a declining trend.

Water quality criteria may be more important than physical structure or habitat features in determining the bay anchovy's well-being, but surprisingly little is known about its vulnerability to anthropogenic inputs of toxicants. Low DO during summer, which limits habitat avail-

ability to all life stages, is potentially an important factor controlling population production of bay anchovy. The "top-down" influence of bay anchovy grazing on plankton and its effect on water quality also are of interest to ecologists concerned with food webs, community structure, and water quality restoration in the Chesapeake Bay.

BACKGROUND

Geographic Range

Two *Anchoa* species occur in the Chesapeake Bay and the mid-Atlantic region: *A. mitchilli* and *A. hepsetus* (striped anchovy). Adults of these species can be differentiated based upon their morphology and fin ray counts.³⁶ Bay anchovies occur along the Atlantic Coast from Maine to the Yucatan Peninsula, including the Florida Keys.^{5,6,18} They may have the largest biomass of any estuarine fish

found along the U.S. South Atlantic and Gulf Coasts.³² Information on bay anchovy life history, environmental requirements, distribution and abundance has been summarized in species profiles.^{69,72,78}

Bay anchovy is the most abundant fish in the Chesapeake Bay^{29,36} and occurs throughout its waters⁴¹ (Map Appendix). Adult bay anchovy migrate during winter to deeper waters in the Chesapeake Bay^{36,86} and to the inner continental shelf in other regions, returning to estuaries in the spring.^{13,33,34,98} Larvae and small juveniles are distributed throughout Chesapeake Bay; some migrate or are transported into low salinity subestuaries, remaining there until fall before dispersing to over-wintering areas.^{24,63,87}

Over its geographic range, bay anchovy is a nearshore, coastal, and estuarine species. It seldom occurs in waters deeper than 25 m,⁸ but has been collected in 27-36 m depths.³⁴ Bay anchovy inhabits both clear and turbid waters and has been collected over all types of substrates, including muddy coves, grassy areas, surf zones, oyster bars, sandy beaches, and sand and silt bottoms.^{5,36,56,80,98}

Bay anchovy is pelagic in all life stages. The reported vertical and horizontal distributions of each life stage are variable and not readily predictable. Dalton¹⁷ reported that mean egg densities were significantly higher in near-bottom samples than in surface samples in the mid-Chesapeake Bay. However, Houde⁴⁶ found both eggs and larvae to be primarily above the pycnocline on two widely separated transects in the Bay. Larval and juvenile bay anchovies in the upper Chesapeake Bay were most abundant near the surface [upper 10 feet (3 m)] from May to October but apparently moved to deeper waters as winter approached.²⁴ Setzler *et al.*⁸⁷ found higher larval densities at shoal stations in the Patuxent River than in channel stations, although the reverse was true for eggs. The depth distributions of larvae in the Patuxent River were complex, varying in relation to larval size, time of day, and river area where they were found.⁶³

Juvenile bay anchovy were collected as much as 40 miles (64 km) above brackish water in Virginia tributaries.⁶⁷ Kaufman *et al.*⁵³ found juveniles were most abundant in near-surface waters in the upper Chesapeake Bay and Kernehan *et al.*⁵⁵ reported that juveniles in the Chesapeake and Delaware Canal were most abundant near surface during the day but in mid- to bottom waters at night. Adult bay anchovies were collected throughout the water column in the Delaware River estuary.⁷⁸ Surface schools of bay anchovy are often seen in the upper Chesapeake Bay⁵³ and in the mid-Chesapeake Bay,⁴⁹ particularly in frontal areas at the mouths of rivers.

Population Status and Trends

Trawling, seining and ichthyoplankton surveys in the Chesapeake Bay all indicate that bay anchovy populations

fluctuate widely from year-to-year. No long-term trend in abundance is apparent.

Peak reported mean densities of anchovy eggs are high,^{17,46,74} ranging from 4.02 m⁻³ to 232.00 m⁻³ in Chesapeake Bay (Table 1). Mean larval densities^{17,46,74} ranged from 0.9 to 76.10 m⁻³ in the Bay (Table 1).

Indices of adult bay anchovy abundance varied more than 100-fold in summer beach-seine surveys from 1958-1989 in low salinity tributaries of Chesapeake Bay.⁶⁶ The 32-year mean abundance index was 25.7 bay anchovies per seine haul. The highest index value was 105.9 in 1967 and the lowest was 0.75 in 1958.⁷³ The 1986 index of 44.3 was nearly four times higher than the 1987 value of 12.1.

Year-round bottom trawl catches in the mid-Chesapeake Bay from 1969-1981⁴¹ indicated that bay anchovy abundance varied seasonally and annually. There were usually two seasonal abundance peaks, one in spring (May) and another in fall (September-November), with the fall peak more than two times higher than the spring peak. Lowest catches occurred in winter. Mean annual catches per tow ranged from a low of 58.5 in 1976 to a high of 973.9 in 1980 (Table 2). The 13-year mean was 708.0 anchovies per tow.

Abundance trends in the mid-Bay trawl surveys⁴¹ were similar to trends in trawl surveys in the lower Bay's York and Rappahannock Rivers¹⁰³ in six of the 12 years of concurrent trawling. Abundances in both surveys were low in 1971, 1972, and 1976 and were generally high in 1977, 1980, and 1981. Mean trawl catches in the York and Rappahannock Rivers ranged from 0 in 1966 to 400 in 1980 (Table 2). Trawl catch-per-unit-effort (CPUE) of bay anchovy in mid-Chesapeake Bay surveys during 1986 and 1987 was almost six times higher in 1986⁷³ (Table 2). Peak abundance occurred in September of each year. Bay anchovy dominated the total fish catch (65%) in numbers during a 1988 trawl survey in the mainstem of Chesapeake Bay's Virginia waters.¹² The CPUE ranged from 19.1 in February to 1,888.7 in December. The mean 1988 CPUE was 584.3 anchovies per tow (Table 2).

LIFE HISTORY

All life stages of bay anchovy are found in the Chesapeake Bay.³⁶ The high abundances of eggs and larvae indicate that the Bay is a major spawning and nursery area.^{17,24,74}

Spawning

Spawning by bay anchovy in the Chesapeake Bay is widespread (Map Appendix) and occurs from May to September, with peak spawning in July.^{17,24,64,74,104} The protracted spawning season may extend throughout the year in southern parts of its range,⁵⁰ but is shorter at higher latitudes. Bay anchovy is a batch (i.e., serial) spawner.

Individual females in the Chesapeake Bay spawn at least 50 times each season, producing a mean of 1,129 ova per batch.¹⁰⁴ Bay anchovies spawn in the evening between 1800 and 2400 hours.^{26,35,64,104} Batch fecundity averages 643-740 eggs per gram of female.^{64,104} Bay anchovies spawn where water depth is less than 20 m⁸¹ in salinities from 0-32 ppt.⁷⁸ Peak spawning in Chesapeake Bay apparently occurs at 13-15 ppt²⁴ and at average surface water temperatures from 26.3-27.8°C.^{49,54} In the Delaware estuary, peak spawning occurred at 22-27°C.⁹⁹

Age I females produced from 92 to > 99% of the eggs spawned in July of 1986 and 1987 in mid-Chesapeake Bay. Thus, a reproductive failure in one year could drastically reduce future numbers of Age I females and have a major impact on egg production.¹⁰⁴

Eggs

The approximately 1 mm fertilized eggs are pelagic, slightly ellipsoid with segmented yolk-mass and no oil globules.^{52,99} Time to hatch was reported as 24 h at 27.2-27.8°C,⁵⁷ but this may have been an overestimate because egg stage duration was 24 h at 25°C⁴⁴ and was approximately 18 h at 28-29°C.⁴⁷ Eggs have been collected in most areas of the Bay and its tributaries (Map Appendix). Egg mortality rates are believed to be high. In Biscayne Bay, Florida, egg mortality averaged 86%.⁶⁰

Larvae

The larval stage may be the most sensitive life stage of bay anchovy in the Chesapeake Bay. Larvae are 1.8-2.0 mm long at hatch.⁵⁷ The yolk sac is absorbed in 27 h at 32°C and in 41 h at 24°C.⁴³ Feeding at 25-28°C was initiated at 3.4 mm length and 2-3 days posthatch.⁴³ Laboratory-reared larvae that were offered a range of food concentrations grew from 0.37-0.59 mm d⁻¹.⁵¹

Bay anchovy larvae enclosed in 3.2 m³ *in situ* mesocosms in the Patuxent River grew 0.39-0.63 mm d⁻¹.¹⁶ Larvae in the Patuxent River were reported to grow at > 0.70 mm d⁻¹ in 1982,²⁹ based on otolith increment counts. Otolith-aged larvae from Biscayne Bay grew 0.43 to 0.56 mm d⁻¹⁶⁰ while those in the Newport River, North Carolina, reportedly grew at 0.25-0.31 mm d⁻¹.²⁸ Larval mortality rates are high. A 25% per day mortality rate was estimated recently in Chesapeake Bay,⁴⁶ compared to an estimated rate of 26-36% per day in Biscayne Bay, Florida.⁶⁰

Juveniles

Juvenile bay anchovies are approximately 25-40 mm long. In mid-Chesapeake Bay their growth rates ranged from 0.20-0.33 mm d⁻¹ in 1986 and 1987.^{71,73} The larval and juvenile stages may be completed in as little as 2.5 months and some Chesapeake Bay young-of-the-year may mature by late summer,⁶⁴ although most apparently overwinter before maturing the following year.¹⁰⁴

Adults

Bay anchovies may live to be slightly more than three years old, although few otolith-aged individuals had survived to that age.^{73,78} Adults may attain a maximum length of 110 mm.³⁴ Mean lengths of adults in mid-Chesapeake Bay⁷³ were 55.0 mm fork length (FL) at age I, 70.7 mm FL at age II and 83.1 mm FL at age III. Average annual mortality rates are high, ranging from 89-95% per year.⁷³ Females are generally more abundant than males in trawl collections.^{73,78,94,98}

ECOLOGICAL ROLE

The bay anchovy plays a key role in the Chesapeake Bay food web. It is a major consumer of zooplankton and a dominant prey item in diets of commercially and recreationally important predatory fish including striped bass, weakfish, bluefish, and summer flounder.^{2,10,39,40,68,85}

The diet of juvenile and adult bay anchovies consists primarily of zooplankton, which are eaten selectively as individual particles. Copepods are the dominant prey.^{78,94,97} Large bay anchovy add macrozooplankton to the diet, such as mysids, larval fish, crab larvae, and other invertebrates, and including some benthic organisms (e.g., polychaetes and molluscs). Small particulates (e.g., algae and detritus) may be found in stomachs of all anchovy length classes.^{1,3,9,19,20,33,40,79,80,89,90,97,101} The dominance of copepods in the diet may be replaced when other potential foods are abundant.²² Feeding may occur throughout the day, but during summer months in Chesapeake Bay it is most intense from dawn to mid-morning.^{40,97} Daily ration was estimated to be 16.2% of body weight.⁹⁷ Food consumption and other energetics parameters were temperature-dependent in the 19-27°C range, with highest consumption and growth at 27°C.⁹⁷

The bay anchovy is preyed upon by seabirds, including the common tern,⁸⁴ and might be an important food item for waterfowl and other animals.²⁴ Bay anchovy provides more than half of the total energy intake of predatory fish in Chesapeake Bay, contributing 70, 90 and 60% to their diets in summer, fall and spring, respectively.²

Potential competitors of bay anchovy are other plankton-eating fishes, including menhaden and silversides. The bay anchovy diet was demonstrated to overlap with that of blueback herring in the James River, Virginia.⁷ Ctenophores (comb jellies) and other jellyfish (e.g., sea nettles) are major consumers of zooplankton in Chesapeake Bay² and may compete for it with the bay anchovy.

The reported first food of larval bay anchovies is microzooplankton, including copepod nauplii, rotifers, and tintinnids.^{21,50} Older larvae fed upon larger copepodites and adult copepods.²¹ Larvae from Biscayne Bay, Florida

ate primarily copepods (75.4%) but included tintinnids, rotifers, and bivalve larvae in their diet.⁵⁰

Larval bay anchovies require food within 2.5 days after hatching at 26°C.⁴³ High larval growth rates and survival rates were obtained at microzooplankton prey levels near ambient and as much as ten-fold below ambient in *in situ* enclosure experiments in the Patuxent River,¹⁶ indicating that food levels in Chesapeake Bay subestuaries generally are adequate for larval production. Based upon laboratory studies, Houde^{44,45} had suggested that 100 microzooplankton per liter was a critical food level for bay anchovy larval survival, but the Patuxent River enclosure experiments indicate that concentrations as low as 50 L⁻¹ may suffice.¹⁶

Bay anchovy eggs and larvae, being the dominant ichthyoplankton in the Chesapeake Bay,^{17,24,74} are believed to interact significantly with many predators and prey. Gelatinous zooplankton, including sea nettles, ctenophores, and other medusae, are predators on eggs and larvae^{15,70} and also may compete with larvae for zooplankton food. Adult bay anchovy may be cannibalistic; they have consumed bay anchovy eggs in experiments.¹⁵ The importance of cannibalism is unevaluated but is a potentially important mechanism of population regulation. The sea nettle, which reaches peak abundance in summer, may be the most effective predator on bay anchovy eggs and larvae in Chesapeake Bay.

HABITAT REQUIREMENTS

Water Quality

Dissolved Oxygen

Dissolved oxygen concentrations below 3.0 mgL⁻¹ probably limit the viability and productivity of bay anchovy in the Chesapeake Bay. Laboratory experiments on bay anchovy eggs and yolk-sac larvae indicated that LC₅₀ was 2.8 mgO₂L⁻¹ for eggs and 1.6 mgL⁻¹ for yolk-sac larvae.¹¹ Egg hatchability declined significantly below 3.0 mgL⁻¹. Survival of newly-hatched larvae declined below 2.5 mgL⁻¹. Many 12-24 h posthatch larvae survived at concentrations between 2.0 and 2.5 mgL⁻¹ and some survived when DO was between 1.0 and 2.0 mgL⁻¹. The long-term consequences of low oxygen on larval survival and growth are unevaluated.

Large volumes of the Chesapeake Bay in summer have median DO below 3.0 mgL⁻¹ and 2.0 mgL⁻¹ (Map Appendix), thus limiting availability of bay anchovy habitat, especially in the Maryland portion of the Bay. Concentrations below 3.0 mgL⁻¹ mostly are confined to depths > 8-10 m (i.e., subpycnocline). In one study, bay anchovy eggs were reported to be abundant at subpycnocline depths,¹⁷ but recent data indicate that few eggs or larvae are found there when DO is low.⁴⁷

Salinity

All life stages of bay anchovy occur over a wide salinity range in the Chesapeake Bay (Map Appendix; Table 3) and in other ecosystems. Eggs in Chesapeake Bay, Delaware Bay, and the Potomac River occurred at salinities from < 1 to 32 ppt.^{24,78,86} Egg viability may be low at salinities below 8 ppt.⁹⁹ Reported suitable salinities for eggs were 4-9 ppt,⁶¹ 1-22 ppt,²⁴ and > 20 ppt.⁷⁸ Highest egg densities were observed at salinities from 13-15 ppt in the upper Chesapeake Bay²⁴ and at 17-23 ppt in the polyhaline lower Bay.⁷⁴ In Delaware Bay higher percentages of live eggs were found in higher salinity waters (20-30 ppt) than in lower salinity waters (< 15 ppt).⁹⁹ Larval bay anchovies occurred in Chesapeake Bay at salinities from 0.0-31.9 ppt^{17,24,74} and were reported at salinities as high as 36.5 ppt in Biscayne Bay, Florida.⁵⁰

Juvenile and adult bay anchovy throughout their range are euryhaline and have been collected in salinities from 0-80 ppt.^{24,67,78,92} Salinity apparently has minor influence on the distribution of bay anchovy.^{31,56,79,93} The preferred salinity range apparently is 9-30 ppt in Chesapeake Bay (Table 3), although adults occur throughout the salinity gradient (Map Appendix) which ranges from 0 ppt²⁴ to 31.9 ppt.⁷⁴

Turbidity and Suspended Sediments

Bay anchovies often live in turbid waters and may be attracted to high turbidities.⁶² No information specific to Chesapeake Bay is available, but significant mortality of adults occurred in static bioassays of fuller's earth suspensions of 2.31, 4.71 and 9.60 gL⁻¹ (10, 50 and 90% mortalities, respectively) after 24 h exposure.⁹¹ Suspended sediment concentrations > 250 mgL⁻¹ caused a reduction in food ingestion by copepods, a primary food of bay anchovy.⁹¹

Temperature

Preferred temperatures for bay anchovy eggs are in the broad range of 13-30°C (Table 4). Eggs have been collected in Chesapeake Bay waters from 9.0-31.0°C,²⁴ indicating a broad tolerance to temperature (Table 4). However, laboratory studies on naturally fertilized eggs indicated that successful incubation temperatures were 17-25°C for eggs collected in the Delaware River.⁷⁸ Seventy-six to 100% of eggs acclimated to 27°C hatched following induced temperature changes of 1.5-7.0°C for 0.5-5.0 h duration.⁷⁸

Preferred temperature ranges for bay anchovy larvae are 15-30°C (Table 4). Larvae tolerated temperatures as high as 35°C in 1-5 minute exposures after acclimation at 17-25°C.⁷⁸ Juveniles in Chesapeake Bay can tolerate temperatures from 0-31°C but may prefer 10.0 to 30.0°C (Table 4).

Adults tolerate a wide range of temperatures (Table 4) in all seasons in Chesapeake Bay where monthly mean

surface water temperatures range from 3.4°C in January to 26.3°C in August.⁵⁴ They occur at temperatures from 2.2-27.1°C in the Hudson River Estuary²⁵ and 16-34°C in the Everglades, Florida.⁸³ Preferred temperatures of adults in Texas estuaries were 8.1-32.2°C,¹⁰⁰ with a possible upper lethal limit of 40°C.¹⁴

Habitat

Structure, except for that associated with water column hydrography, is not believed to be important for the pelagic bay anchovy. In Chesapeake Bay, the anoxic or hypoxic (< 3.0 mgO₂L⁻¹) waters below the pycnocline during summer (Map Appendix) may limit habitat available to all life stages and may force bay anchovies to be distributed nearer to the surface than otherwise.

Substrate

Bay anchovy has been collected over many substrates, including sand, mud, sea grass, oyster shell, and the hard bottoms of beaches in surf zones.^{5,36,56,80,98} There is no indication that it prefers any particular substrate.

Vegetation

Seagrass beds in Chesapeake Bay were not important spawning sites for bay anchovy or other fishes that produce pelagic eggs.⁷⁵ There also is no indication that they are important nursery areas for bay anchovy larvae.

Depth

Bay anchovy has been collected from waters as deep as 27-36 m,³⁴ although it generally occurs in shallower depths. Eggs have been collected throughout the water column (surface to > 20 m depth) in the Chesapeake Bay.^{17,46} Unpublished information⁴⁶ indicated that egg densities were 6.5 times higher above the pycnocline than below it, and that larval densities were 8.4 times higher above the pycnocline. Small larvae tended to remain farther below the surface in the Patuxent River mouth than did > 11 mm larvae, which showed no depth preference.⁶³ Upstream in the Patuxent, the larval depth distribution and factors influencing it became more complex.⁶³

Juvenile and adult bay anchovy may occur throughout the water column in Chesapeake Bay⁴⁸ and Delaware Bay.⁷⁸ There is some published evidence that schools tend to be located nearer to surface than to bottom,^{53,55} but recent hydroacoustic surveys⁴⁸ indicate that changes in depth distribution occur, both seasonally and diurnally, that are not well understood.

Weather

Seasonal changes in water temperatures may cause offshore migrations during winter by bay anchovy in the temperate parts of its range.⁹⁸ It is not certain whether winter temperatures induce offshore migration of some Chesapeake Bay anchovies. Some bay anchovies were collected by otter trawl during all months in a 13-year

program in the mid-Chesapeake Bay.⁴¹ Trawling surveys after tropical storm Agnes in June, 1972, indicated that adult bay anchovy abundance was not affected in the middle or southern portions of the Chesapeake Bay.^{82,88} Large numbers of bay anchovy larvae may have been swept out of the James and Rappahannock Rivers into the Bay during the flood following the storm.³⁷ Dalton¹⁷ found two peaks in egg abundance during 1972, one before and one after tropical storm Agnes. Egg abundances were low 30 days after the storm and the 1972 annual mean larval density was 18 times lower than the mean density for the four years of 1972, 1974, 1976, and 1977.

SPECIAL PROBLEMS

Contaminants

Despite the bay anchovy's abundance, there is surprisingly little information on toxicants. Contaminant problems from use of chlorine in power plant⁷⁸ and sewage plant discharges may be problematic. Bay anchovy was the dominant fish within areas of Galveston Bay that reportedly received highest pollutant loads,³ suggesting to the authors that the bay anchovy dominance might be an indicator of pollution stress.^{3,69} The increased turbidities associated with kraft pulp mill effluent, which contained toxins, may have attracted bay anchovies, despite the pollutant level.⁶²

Parasitism and Diseases

Unidentified parasitic trematodes were found in 19.3% of Chesapeake Bay adult bay anchovy stomachs in 1986 and 1987.⁹⁷ Parasitic copepods are frequently observed on bay anchovy, especially in summer and fall.^{58,59} A parasitic brachyuran (crab) also has been observed attached to larval and juvenile bay anchovies.⁷⁸ Fin-rot disease on bay anchovies in New York Bight was attributed to dense bacterial populations and environmental stress from domestic and industrial pollution in 1967-1971.⁶⁵

Power Plant Entrainment and Impingement

The abundance, small size, and widespread occurrence of bay anchovy make all life stages vulnerable to entrainment in power plant cooling waters or impingement on screens designed to prevent entrainment of organisms.^{42,76,78,95} On-site studies in the Delaware River estuary⁷⁸ indicated that most anchovy eggs and larvae were entrained from May through October. Juveniles and adults were entrained in all months except February and December. Numbers entrained were sometimes high.

Most mortality in both intake and discharge samples at a Delaware River power plant occurred in the first six hours following entrainment although some mortality continued for at least 24 h⁷⁸ (Table 5). In laboratory studies that simulated the mechanical stress of entrainment, mortality was significant for all life stages except prolarvae.

Mortality of early life stages was variable, but tended to increase as the temperature differential in simulated cooling waters increased.⁷⁸

Simulation models were used to predict bay anchovy entrainment losses at a power plant on the Patuxent River near Chalk Point.⁷⁶ A reduction in juvenile survival of up to 76% was possible, primarily from losses during the postlarval stage (10-35 mm), because that stage was concentrated where entrainment probability was highest. The authors⁷⁶ believed that the probable range of loss due to entrainment was 24-76%.

Another simulation model⁹⁵ for the same power plant predicted that bay anchovy standing stock might decline by 46% and that predatory fish, such as striped bass, bluefish, and weakfish could experience standing stock losses of > 25% if bay anchovy and silversides were the preferred prey and if their entrainment losses were $\geq 70\%$. If, as seems likely, the entrainment losses were lower, perhaps only 30%, then bay anchovy standing stock would decline by 21% and piscivorous fish standing stock by 10-15%. If anchovy and silversides were not the major component of predator diets, then losses of predator production would be small.

Bay anchovy was the most common species impinged at a nuclear power plant in mid-Chesapeake Bay from 1975-1983.⁴² Most impingement occurred from April-June and in November; the least occurred in February and March. Bay anchovy had intermediate rates of survival (45-90%) compared to other impinged species. The estimated number of anchovies impinged annually ranged from 5,219 (in 1982) to 1.1×10^6 (in 1981). Age I fish were the dominant group impinged. Horwitz⁴² noted that the consequences of impingement mortality depend upon its magnitude relative to other sources of mortality; he concluded that impingement mortality at the Chesapeake Bay nuclear power plant probably was small relative to total mortality.

RECOMMENDATIONS

Although there is no evidence of population decline or instability in the bay anchovy population in the Chesapeake Bay, there are concerns. Two recommendations may improve habitat conditions and insure future well-being of the bay anchovy population.

- 1) Reduce the volume of water that becomes anoxic or hypoxic ($< 3.0 \text{ mgO}_2\text{L}^{-1}$) during summer and thereby ex-

pand the productive habitat of all life stages of bay anchovy. Also, reduce the frequency of transient, low DO events ($< 2.0 \text{ mgL}^{-1}$) through appropriate Baywide nutrient reduction strategies.

- 2) Carefully consider the siting of proposed power plants that may entrain and impinge all life stages of bay anchovy, potentially affecting not only anchovy productivity but also that of large, predator fishes that depend upon bay anchovy as food.

Some research recommendations that will enhance our knowledge of this key species and its sensitivity to habitat change in Chesapeake Bay include:

- 1) Determine the sensitivity of all life stages to potential toxicants.
- 2) Estimate the biomass and production of bay anchovy, and their annual variability.
- 3) Estimate the amounts and kinds of plankton consumed by the bay anchovy population on an annual basis to determine its potential "top-down" control on plankton production, community structure, and water quality.
- 4) Determine the fraction of the standing stock of bay anchovy consumed annually by predator fish to quantify its key role in the Bay's food web.

CONCLUSIONS

The bay anchovy is abundant and ubiquitous in the Chesapeake Bay where it plays a key role in the food webs of the plankton and pelagic fish communities. The bay anchovy population is in no immediate danger of decline from present habitat conditions or water quality, but it is important to be alert for potentially deleterious effects of toxicants, power plant operations, and nutrient pollution causing summer hypoxia. The population dynamics and trophic relationships of bay anchovy in Chesapeake Bay are just beginning to be understood. A better knowledge of bay anchovy's role in the Bay trophic structure will be important for long-term management of Chesapeake Bay water quality and fish resources.

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Table 1. Summary of mean bay anchovy egg and larval densities. Collections were made with various types of sampling gear. Life stage: E = eggs; L = larvae; A = adults.

Location	Time period	Life stage	Peak density #/100 m ³	Percent of total catch	Reference
Barnegat Bay, N.J.	1975-1981	E	13250 ^a	98	98
		L	1120 ^a	56	
		A		52	
Biscayne Bay, Fl.	1976-1977	E	10150 ^a	55.8	50
		L	246 ^a	20.1	
mid-Chesapeake Bay	1972-1977	E	3500 ^b	99	17
		L	200 ^b		
lower Chesapeake Bay	1971-1976	E	14000 ^a	96	74
		L	2403 ^a	88	
mid-lower Chesapeake Bay	1987	E	23200 ^c		46
		L	7610 ^c		
upper Chesapeake Bay	1963-1967	E	43000 ^d		24
Patuxent River	1960-1971	L	16400 ^d		25
	3/78/8/78	E	402 ^a		87
		L	38 ^a		
Potomac River	1974-1976	L	90 ^d		86
Hudson River	4/72-8/72	E		99.8	25
		L	23600 ^d	70	

^a monthly mean^b 1974 average^c cruise and station mean^d single collection

Table 2. Summary of bay anchovy abundance in Chesapeake Bay. Indices are counts of fish per unit effort.

Location	Years	Gear	Unit effort	Range of abundance index	Reference
low-salinity tributaries	1958-1989	beach seine	haul	0.75(1958)-105.9(1967) ^a	73 ^c
mid-Bay	1969-1981	7.6 m balloon trawl	30 min. tow	58.5(1976)-973.9(1980) ^a	42
York and Rappahannock Rivers	1955-1982	30 ft. semi-balloon trawl	5 min. tow	0(1966)-400(1980) ^a	103
mid-Bay	1986-1987	4.9 m semi-balloon trawl	10 min. tow	54(1987)-354(1986) ^a	73
Virginia mainstem Bay	1/88-12/88	30 ft semi-balloon trawl	5 min. tow	19.1(Feb.)-1888.7(Dec.) ^b	12

^a mean annual abundance.^b annual mean = 584.3; bay anchovy were 65% of the total number of fish caught.^c MDNR data 1958-1989 cited in 73.

Table 3. Salinity ranges for bay anchovy occurrence.

Life stage	Minimum salinity ppt	Maximum salinity ppt	Preferred or optimum range (ppt)	Location	Reference
EGGS			4.0-20.0	overall suitable range	
	1.0	22.0	13.0-15.0	upper Chesapeake Bay	24
			4.0-9.0	Potomac River	61
	0.0	32.0	> 20.0	Delaware River estuary	78
	< 1.0		6.0-10.0	Potomac River	86
	> 8.0		20.0-30.0	Delaware River estuary	99
	6.4	31.9	17.0-23.0	lower Chesapeake Bay	74
LARVAE			0.0-15.0	overall suitable range	
	0.0		3.0-7.0	upper Chesapeake Bay	24
			4.2-6.0	Hudson River	25
	6.4	31.9		lower Chesapeake Bay	74
	0.0	31.0	0.0-> 5.0	Potomac River	61
	0.0	49.0		Delaware River estuary	99
				Alazan Bay, Texas	23
JUVENILES			9.0-30.0	overall suitable range	
	≤ 0.5 ^a			Delaware River estuary	77
			3.0-7.0	upper Chesapeake Bay	24
ADULTS	> 2.3		20.8-37.6	Florida Gulf coast	56
			9.0-30.0	overall suitable range	
			13.0-15.0 ^b	upper Chesapeake Bay	24
			13.5-15.3 ^c	mid-Chesapeake Bay	49
			1.0-32.0	Matagorda Bay, Texas	100
	0.0			Virginia tributaries	67
	< 0.5 ^d			Delaware estuary	77
		75.0-80.0	< 50.0	Laguna Madre, Texas	92
	> 5.0 ^c		10.0-20.0 ^c	Delaware River estuary	99
	15.5	45.2		Florida Everglades	83

^a at temperature > 20°C^b peak spawning^c spawning^d laboratory tests: bay anchovies were unable to survive below 0.5 ppt for extended periods. Mortality: 70% in 4 h at 24°C, 73% in 2 h at 23°C, 30% in 96 h at 10°C.

BAY ANCHOVY

Table 4. Temperature ranges for bay anchovy.

Life stage	Minimum °C	Maximum °C	Preferred or optimum range	Acclimation °C	Location	Reference
EGGS	9.0	31.0	13.0-30.0		overall suitable range	
			20.0-27.0		upper Chesapeake Bay	24
			27.2-27.8		Beaufort, North Carolina	57
			17.0-25.5		Delaware River estuary ^h	78
			22.0-32.0		Miami, Florida	21
			27.2-27.8		Matagorda Bay, Texas	100
LARVAE	7.0 0.0	31.0	15.0-30.0	25 (15ppt)	overall suitable range	
			40.0 ^a		Delaware River estuary	78
			> 11.0		Matagorda Bay, Texas	100
			23.0-27.0		Alazan Bay, Texas	23
JUVENILES	0.0	31.0	10.0-30.0		overall suitable range	
			26.0-28.0		upper Chesapeake Bay	24
			20.0-24.0		Delaware River estuary	78
					New Jersey	96
	6.0-15.0	29.0-31.5 ^b 31.5-32.0 ^c 31.5-32.0 ^c 31.0-35.0 ^d 25.0-33.0 ^d 34.0-37.0 ^e 32.0-35.0 ^e		10 and 25 19.5 and 24.0 19.5 and 24.0 10 and 25 24.6-31.3 15.0-26.4 summer winter	Delaware River estuary	77
ADULTS	2.2 10.0 ^f	37.0 27.1 > 32.0	5.0-30.0		overall suitable range	
			24.5-32.5		Galveston Bay, Texas	30
					Hudson River	25
					New Jersey	96
	16.0 > 15.0 ^g	34.0 30.0	20.0	22 (30 ppt) 21 (28 ppt) 15 (29 ppt)		
			27.0			
			8.1-32.2		Delaware River	78
					Matagorda Bay, Texas	100
		> 40			Galveston Bay, Texas	14
					Florida Everglades	83
		30.0	22.0-27.0 ^g		Delaware estuary	99
			27.2-27.8 ^g		mid-Chesapeake Bay	49

^a lethal

^b 48 h LT₅₀

^c LT₁₀₀

^d 3 h LD₅₀

^e 0.5 h LD₁₀₀

^f total mortality at 29 h

^g spawning

^h for successful incubation

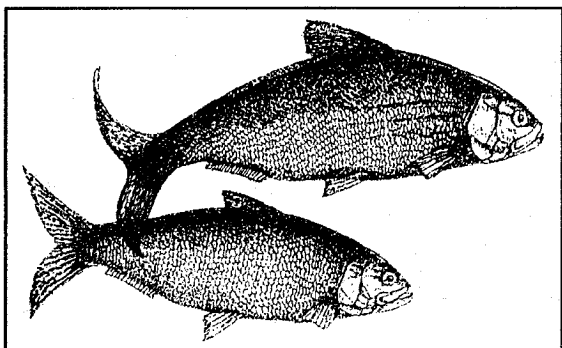
Table 5. Summary table of on-site entrainment survival studies at a Delaware River power plant.⁷⁸

Life Stage	Initial Survival %	12-h Survival %	24-h Survival %	Delta T °C	Ambient River T °C
Intake Larvae	31.2-87.5	0.0-17.5	0.0-5.0	0.0-14.0	15.0-31.6
Discharge "	0.0-37.2	0.0-16.7	0.0	" "	
Intake Juveniles	75.0-100	0.0-66.0	0.0-30.7	0.0-14.2	10.0-31.6
Discharge "	12.5- 87.4	0.0-48.7	0.1-14.2	" "	
Intake Adults	62.0-84.0	28.0-77.8	1.2-16.9	0.5-14.0	11.5-31.6
Discharge "	35.3-68.2	0.0-50.0	0.0-33.3	" "	

AMERICAN SHAD AND HICKORY SHAD

Alosa sapidissima and *Alosa mediocris*

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American shad and hickory shad are anadromous fish of the clupeid family. American shad are the largest anadromous clupeids of the U.S; hickory shad are medium-sized members of the family. Natural shad spawning habitats include non-tidal reaches of virtually all Chesapeake Bay tributaries. American shad juveniles leave the estuary in late fall, mature in the ocean, and return to the tributaries to spawn after two to five years. The life history of hickory shad is similar, but poorly known.

American shad historically supported important recreational and commercial fisheries in Chesapeake Bay

tributaries, whereas hickory shad, because of their naturally lower abundance in the region, were a much less important fishery species. Severe stock declines of both species in the latter half of the 20th century led to drastically lower harvests, and a fishing moratorium in the Maryland portion of Chesapeake Bay which has been in effect since 1980. The causes of the declines apparently include overfishing in earlier decades, blockage of spawning rivers by dams and other impediments, and degradation of water quality and physical habitat in spawning reaches.

The critical life stages of shad are the eggs, larvae, and early juveniles. Water temperatures $> 13^{\circ}\text{C}$, $\text{pH} > 6.0$, and dissolved oxygen $> 5.0 \text{ mgL}^{-1}$ are important requirements for American shad eggs. Larvae require water temperatures of $15.5\text{--}26.1^{\circ}\text{C}$, $\text{pH} > 6.7$, dissolved oxygen $> 5.0 \text{ mgL}^{-1}$ and suspended solids $< 100 \text{ mgL}^{-1}$. Requirements of juvenile American shad are similar to those of larvae. Insufficient information is available to make definitive statements about the habitat requirements of hickory shad, but they probably are similar to those of American shad. Major habitat concerns for shad are stream acidification and interaction with dissolved metals, stream blockages, and land disturbance with associated sedimentation and turbidity.

Although American shad have shown some signs of recovery in recent years, stocks must continue to be protected, both from excessive harvest and from degradation of their spawning and nursery habitats. Continuing removal and mitigation of stream blockages, stocking programs, and harvest restrictions are positive steps toward recovery of these threatened populations.

INTRODUCTION

The American shad is the largest anadromous fish of the clupeid family in the United States. Maximum length is

about 760 mm.⁶⁴ American shad have a deep and laterally compressed body, single soft-rayed dorsal and anal fins, and large easily-shed scales that come together to form saw-toothed scutes along the ventral margin of the belly.

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AMERICAN SHAD AND HICKORY SHAD

Adults are silvery white on the sides, with greenish or bluish coloration above that fades to brown as they migrate through freshwater to spawn. The large black spot located just behind the gill cover is followed by several (4-27) smaller dark spots.¹³¹

The hickory shad is a medium-sized anadromous clupeid that is smaller than the American shad but larger than the alewife and blueback herring. Maximum length is about 600 mm.⁶⁴ The hickory shad is distinguished from the other anadromous clupeids by a strongly projecting lower jaw and small number of gill rakers, usually 19-21, on the lower limb of the first pharyngeal arch.^{56,97} Hickory shad are gray-green along the back, with iridescent silver sides and belly. The dark shoulder spot commonly is followed by several obscure spots.^{64,96}

DISTRIBUTION

The American shad is native to the Atlantic seaboard of North America, distributed from southeastern Labrador to the St. Johns River, Florida.^{64,131} Along the east coast of the United States, American shad are most abundant from Connecticut to North Carolina.⁹⁹ In the mid-Atlantic region, American shad historically spawned in New Jersey, Delaware, and virtually all major tributaries to Chesapeake Bay. The presence of spawning populations in several Maryland tributaries has been difficult to document in recent years.⁷³

In 1871, American shad fry were transported successfully by rail from the Atlantic Coast to the Pacific Coast and introduced into the Sacramento River, California.¹²⁴ Other Pacific Coast introductions followed in the Columbia, Snake, and Willamette rivers in 1885 and 1886.¹²⁰ From these introductions, American shad dispersed and populations are now established from Baja, California, northward to Cook Inlet, Alaska, and the Kamchatka Peninsula, Asia.^{53,131} Attempts to introduce American shad into the Mississippi River drainage and streams in Florida were apparently unsuccessful.¹¹

Historically, the hickory shad occurred along the east coast of North America from the Bay of Fundy, Canada, to the Tomoka River, Florida; but now the species probably is restricted to waters from New York southward^{5,55,97,124} and is viewed as a more southern species than American shad.⁷³ Their current presence in Canadian waters is uncertain; they are not listed in a recent book on Atlantic fishes of Canada.¹³¹ Overview documents prepared by state fisheries agencies along the east coast of the United States suggest that hickory shad currently do not spawn north of Maryland.¹²² In Chesapeake Bay, hickory shad are near the northern limits of their spawning range and probably never have been abundant,¹³⁵ although they were harvested throughout the Bay prior to the 1970's.⁹⁷ Stable or declining stocks are present in the majority of

coastal river systems in North Carolina, South Carolina, Georgia, and Florida.¹²⁴

LIFE HISTORY

AMERICAN SHAD

The American shad is anadromous, lives at sea, and only enters freshwater in the spring to spawn. It is a schooling species and highly migratory. Each major shad-producing river along the Atlantic seaboard appears to have a discrete spawning stock.¹² Homing to the natal stream is relatively well documented in northern stocks¹³¹ such as those of the Connecticut and Hudson rivers, and involves both olfaction and rheotaxis.⁴¹ However, there is evidence of extensive straying, particularly on the West Coast of the U.S.⁷³ Straying and mixing also may occur among American shad stocks which use a large and diversified estuarine system such as the Chesapeake Bay.

Spawning Activity

American shad migrate from the sea to coastal rivers in the spring for spawning when water temperatures range from about 16-19°C.⁷⁹ Some adults enter the mouths of their natal rivers when temperatures are as low as 4°C or less.⁶⁴ The prespawning adults spend one or two days meandering near the saltwater-freshwater interface during a necessary period of adaptation before proceeding upstream to spawn.⁴¹

American shad can spawn as early as mid-November in Florida (typically not before February) to as late as July in some Canadian rivers.⁹⁵ If possible, the adults migrate far upstream and typically spawn in freshwater areas dominated by extensive flats and over sandy or rocky shallows,⁶⁴ including the mouths of larger tributary streams.³⁹ Males generally precede the females to the spawning grounds.²⁵

Water temperature is the primary factor that triggers spawning, but photoperiod, current velocity, and turbidity also exert some influence.⁷⁹ In Chesapeake Bay, spawning runs typically begin in mid-February to early March, peak during April, and are over by early June.^{55,64} Egg deposition has been observed at water temperatures between 8 and 26°C, but most spawning in Chesapeake Bay rivers occurs between 12 and 21°C.^{64,148}

Most spawning activity occurs between sunset and midnight, with the time of onset related to light intensity.^{110,131} In turbid rivers, spawning also may occur during daylight hours.⁶⁴ American shad are broadcast, open water spawners. During the spawning act, a single female is accompanied by several males as the eggs are released into the water column and fertilized.^{100,108} Adults return to the sea soon after spawning.²⁶

Egg and Larval Development

Fertilized eggs are spherical, semi-demersal to pelagic, non-adhesive, from 2.5-3.5 mm in diameter when water-hardened, and transparent pale amber or pink.⁶⁴ As American shad eggs water-harden and increase in diameter, they are carried by river currents along the bottom and may lodge in substrate rubble.

Egg incubation time can range from two days at 27°C, from three to nine days at 22-17°C, to 17 days at 12°C.⁶⁴ Optimum conditions reported for American shad egg development are 17°C, 7.5 ppt salinity, and darkness.⁸⁰ Maximum egg survival and hatching success is in the temperature range of 15.5-26.5°C.⁷⁹ Egg development can be prolonged and mortality increased when incubation temperatures fall below 16°C.¹⁰⁰ No viable eggs developed at temperatures below 10°C or above 29°C.^{80,8} American shad eggs incubated at temperatures between 20.0 and 23.4°C hatched in three to five days, but the resulting yolk-sac larvae were deformed.⁸⁰

Yolk-sac larvae are 6-10 mm total length (TL) at hatching and 9-12 mm TL when the yolk is absorbed at four to seven days old and the larvae begin to feed exogenously.^{101,152} The larvae are photopositive,⁶¹ most abundant near the surface in fresh and brackish waters up to about 7 ppt salinity,^{101,97} and generally drift downstream and disperse as they develop.⁴⁹

Natural mortality rates during the egg and larval stages of American shad are very high. Leggett⁷⁶ reported that, on average, only 0.00083% of the eggs spawned produce sexually mature adults. Most of this high mortality occurs between egg deposition and the juvenile stage. Survival from the yolk-sac larva through the juvenile stage is about 1 to 2%. Year class strength for cohorts in American shad populations is apparently established during the first 20 days after hatching and before the larvae reach the juvenile stage.³² Availability of food is critical to the survival of first feeding larvae, but other environmental factors also are important. Recent studies suggested a relationship between water temperature, flow, food production, food density, and the survival of American shad larvae.⁷³

Juveniles

Metamorphosis or transformation to the juvenile stage is completed in about 21-28 days when the young American shad reach 25-28 mm TL.³⁰ They form schools at 20-30 mm TL and prefer deep pools away from the shoreline in non-tidal areas, although they occasionally move into shallow riffles.²⁰ In the Chesapeake Bay system, juveniles spend their first summer in tidal freshwater reaches of the spawning rivers.

Juvenile American shad undergo diel vertical migrations in the summer nursery areas. Loesch *et al.*⁹⁰ observed that catches of juveniles in bottom trawls were significantly

higher during the day than at night. Conversely, catches of juveniles in surface trawls were greater at night than during the day.

Autumn decreases in water temperatures below 19 or 20°C, increases in river flow, or combinations of both factors trigger downstream movements of juvenile American shad through brackish water and on to the sea.^{21,148} Peaks in the seaward migration of juveniles in the Chesapeake Bay region occur from late October to late November⁹⁵ when water temperatures are below 15°C. Decreasing water temperatures may curtail the behavioral tendency of juveniles to maintain position against the current in low light or at night, and consequently, they drift downstream.¹¹⁸

Several investigators have reported that larger juveniles appear to move downstream earlier in the fall.^{20,101,127} Juvenile American shad grow to average lengths ranging from about 80-110 mm prior to the fall seaward emigrations.^{101,124,127} Growth of juveniles appears to be slower in more southerly rivers along the U.S. east coast.¹⁰¹

Estimates of juvenile American shad mortality rates in the nursery areas range from 1.8-2.0% per day.³² Thus, if the juveniles remain in the nursery areas for three months before emigrating seaward, their survival rate would be about 30%. Conversely, 70% of the juveniles would perish before reaching the ocean,¹²² assuming constant mortality rates during the larval and juvenile stages. Longer residence times in freshwater and brackish areas would further reduce first year survival of American shad cohorts.

Subadults and Adults

Juvenile American shad leave the nursery areas in late fall and presumably join other schools of young shad in the ocean, where they grow and develop for three to five years before returning to their natal streams to spawn.¹¹² Chesapeake Bay stocks remain at sea for about four or five years; however two-year old fish have been collected in the Bay.⁷³

American shad are long-distance coastal migrants. During an average life span of five years at sea, an individual may migrate over 20,000 km.³⁵ Ocean migration rates estimated from tag returns averaged 21 km d⁻¹ during the spring northward migrations of adults from Chesapeake Bay to the Bay of Fundy,⁷⁶ and about 9 km d⁻¹ for spent adults during a more recent tagging study.³⁵ Subadults appear to migrate farther offshore than sexually mature adults.¹¹²

American shad in the Atlantic Ocean tend to follow preferred isotherms of 13-18°C as they move along the Atlantic coast between summer feeding grounds in the Gulf of Maine and coastal overwintering areas off the mid-Atlantic states.⁷⁹ Dadswell *et al.*³⁵ reviewed 50 years

of tagging studies and concluded that oceanic migration patterns of American shad were more complicated than previously thought. They suggested that American shad stocks do not concentrate in relatively small geographic areas and do not migrate together at the same rate. They also argued that origin, life history characteristics, and chance may be more important in the control of coastal migrations than ocean temperatures.

American shad may grow about 100 mm per year until they reach sexual maturity; then their growth slows to about 50 mm per year through adult life.⁹⁵ Size at age is typically greater in females than males in Chesapeake Bay⁷³ and elsewhere, and greater in northern stocks than southern stocks. The north-south stock difference appears to be genetically controlled.^{77,122} Adult American shad from northern stocks also live longer than adults from more southern stocks. Melvin *et al.*¹⁰⁹ caught a male and female in the Annapolis River, Nova Scotia, that were 12 and 13 years old. American shad from mid-Atlantic populations live for seven to nine years,¹²⁴ but most adults are ages six and seven.

There is a paucity of information on age at maturity for American shad, in general, and none for stocks in the Chesapeake Bay system.⁷³ The available data suggest that males reach maturity at four or five years old, about one year earlier than females.^{93,148} American shad collected in the Susquehanna River and Flats region of Maryland are generally mature by age three (males) and age four (females), according to Weinrich *et al.*¹⁵⁰ Females from Canadian populations tend to mature at a younger age than females from mid-Atlantic stocks, but there is no clear latitudinal gradient in age at maturity along the Atlantic seaboard.⁷⁷

For frequency of repeat spawning, there is a clear latitudinal gradient.^{148,77} In southern stocks (Florida, Georgia, South Carolina), the adults die after their first spawning and repeat spawning does not occur. Repeat spawning occurs at very low frequencies (< 5%) in North Carolina stocks.¹²² During the 1970's, repeat spawning (males and females combined) increased progressively along the Atlantic Coast to 20% in the Potomac River, Maryland; 23% in the York River, Virginia; 27% in the James River, Virginia; 37% in the Susquehanna River, Maryland and Pennsylvania; 57% in the Hudson River, New York; 63% in the Connecticut River; and 73% in the St. John River, New Brunswick.⁷⁷

In recent years, the percentage of repeat American shad spawners in the Susquehanna River region of the Chesapeake Bay has been relatively low.¹⁵⁰ Repeat spawning for males and females combined, 1980-1984, ranged from 2.7% (1981) to 12.14% (1980). Because repeat spawning is so low in Maryland stocks, the size of the spawning run in one year is more a function of the spawning success in

prior years than of the contribution of repeat spawners. This stock condition argues for limitations on fishing exploitation to allow an increase in repeat spawning.⁷³

Fecundity in American shad is relatively high and typically ranges from about 100,000-600,000 eggs per female depending upon length, weight, age, and origin of the fish.¹²⁴ In the York River, Virginia, and the Potomac River, Maryland, fecundity ranged from 169,000-525,000 eggs per female during the 1950's.¹⁴⁸ A trend toward higher fecundity per unit body weight in southern American shad stocks compared to northern stocks has been observed. This latitudinal trend in fecundity can be viewed as an evolutionary adaptation which could compensate somewhat for the opposite latitudinal trend in frequency of repeat spawning.

HICKORY SHAD

The hickory shad is somewhat of a mystery to fishermen and ichthyologists because so little is known about its general life history. Most detailed information comes from studies in Maryland, Virginia, North Carolina, and Georgia.^{1,36,47,49,73,97,103,119,122,124,126,138}

Spawning Activity

As recently as the early 1950's, some ichthyologists speculated that hickory shad spawned in salt water and did not ascend freshwater streams in the Chesapeake Bay system to spawn.⁹⁷ This perception, later disproved, was inspired by the relative scarcity of juveniles in freshwater and brackish habitats. We now understand that hickory shad are anadromous and begin to ascend freshwater streams for spawning in early spring when water temperatures reach 12 or 13°C. Spawning can occur between March and early June, depending upon latitude, over a water temperature range of 12 to 22°C.¹²⁴ Peak spawning occurs during April and May when water temperatures are between 15-19°C.^{96,97,119,126,138} In Chesapeake Bay, hickory shad spawning runs may precede American shad runs and typically begin during March and April.¹³⁵ Peak spawning activity occurs between late April and early June¹³² when water temperatures reach 22°C.⁷³

Specific spawning sites in the Chesapeake Bay are not well documented.¹²² Mansueti⁹⁷ concluded that hickory shad spawned about 6-10 km upriver from the major spawning sites for American shad in the mainstem of the Patuxent River, Maryland.

In Virginia, the major hickory shad spawning sites are in mainstem rivers at the fall line, but some appear to spawn further downstream and also in tributaries.³⁹ In 1967, gravid or ripe hickory shad were collected in the mainstem of the Mattaponi River, between river miles 35 and 54, and in the mainstem of the Pamunkey River, between river miles 45 and 67.³⁷ In 1968, gravid or ripe fish were collected in the mainstem and tributaries of the Rappahan-

nock River, between river miles 31 and 95, during April and May.⁴⁰ The same report also listed a catch of two ripe male hickory shad in the mainstem Potomac River at river mile 99. The James River was surveyed in 1969.³⁸ Ripe or gravid hickory shad were collected in the mainstem, in tributaries between river mile 40 and 59, and also in the Appomattox River. Hickory shad have been observed spawning in the James River at the fall line near Richmond.

The major spawning sites for hickory shad in North Carolina are in the freshwater reaches of coastal rivers.¹⁰³ Pate¹¹⁹ surveyed hickory shad spawning sites in the Neuse River, North Carolina, and collected eggs and larvae only in flooded swamps and sloughs off the channels of tributary creeks and not in the mainstem river. Hickory shad apparently spawn in flooded areas off the channel of the Altamaha River, Georgia, and not in the mainstem of the upper reaches.¹

During peak spawning activity, probably between dusk and midnight, hickory shad eggs apparently are broadcast into the water column and fertilized by accompanying males.^{97,64} We could find no other information on hickory shad spawning behavior.

Egg and Larval Development

The early development of hickory shad was described by Mansueti.⁹⁷ The eggs are slightly adhesive and semi-demersal in slow-moving waters, but partially buoyant under more turbulent conditions.⁹⁸ The fertilized and water-hardened eggs are transparent, spherical, and range from 0.96-1.64 mm in diameter.⁹⁷ Egg development is characterized by meroblastic cleavage and a pattern of embryonic differentiation similar to that found in other clupeid eggs. Incubation time ranges from 48-72 h at temperatures between 21 and 18°C.

Newly-hatched larvae are typically clupeid-form and slender, with a large granulated yolk-sac in the anterior quarter of the body, relatively large eyes, and a transparent body with sparse pigmentation. Size at hatching ranges from 5.2-6.5 mm TL. At four to five days old and 5.5-7.0 mm TL, the yolk is fully absorbed, and the postlarvae are ready to feed exogenously. Mansueti⁹⁷ observed high mortality in laboratory-reared larvae after yolk absorption; none of the larvae could be induced to feed. Postlarvae transform to juveniles when 10-35 mm long.^{146,73}

Juveniles

Young hickory shad 9-20 mm TL are difficult to distinguish from the young of other anadromous alosids such as American shad, alewife, and blueback herring.⁹⁷ As hickory shad grow beyond 20 mm TL, the strongly projecting mandible, straight dorsal profile, and low number of gill rakers on the first arch serve as important diagnostic characters.

Collections of juvenile hickory shad are sparse.^{97,124} The fragmentary records suggest that most young fish leave their freshwater and brackish habitats in early summer and migrate to estuarine nursery areas at an earlier age than other anadromous alosids.^{197,104,133} This conclusion is supported by catches of juvenile hickory shad in a surf zone off Long Island, New York, from April to November.¹²⁵ Studies in the Neuse River, North Carolina¹¹⁹ suggested that young hickory shad may migrate directly to saline areas and not use the oligohaline portion of the estuary as a nursery area. The freshwater zone which forms on the scales of anadromous clupeids is difficult to see on scales from adult hickory shad.

A hypothetical growth curve for hickory shad developed by Mansueti⁹⁷ suggested that juvenile growth during the first season in the Patuxent River, Maryland, exceeded that of the other three alosid species. Growth curves for male hickory shad collected during 1970 in Octoraro Creek, Maryland, showed rapid growth rates during the first three years of life, similar to growth rates for hickory shad in the Altamaha River, Georgia, and Neuse River, North Carolina.¹²⁶ By age III, 79% of the growth in length was completed for the Octoraro Creek males. Juvenile hickory shad collected during bottom trawl surveys conducted by the Virginia Institute of Marine Science (VIMS) in the Rappahannock River, Virginia, during 1968 and 1969, averaged 73 mm in July and August, and 118 mm in September.² One juvenile collected in October 1968 measured 138 mm. The larger size of juvenile hickory shad compared to the other alosid species may be due to the earlier spawning time for hickory shad and a faster growth rate. Juvenile hickory shad collected in the Altamaha River, Georgia,¹ averaged 81 to 90 mm fork length (FL) during July and August. Additional data on juvenile hickory shad growth in southeastern U.S. rivers is presented in Rulifson *et al.*¹²⁴

We could find no information on mortality rates for juvenile hickory shad.

Subadults and Adults

When young hickory shad leave the spawning areas and, presumably, move quickly through estuarine waters to the sea, their life history becomes very obscured. Hickory shad were mature by 287 mm TL (males), 320 mm TL (females), and at about age III in the Patuxent River, Maryland, in 1954.⁹⁷ Adults in this spawning run ranged from about 290-450 mm TL. From spawning checks, Schaeffer¹²⁶ concluded that about 80% of the male hickory shad collected in Octoraro Creek, Maryland, in 1976, matured at age II, with the rest maturing at age III. Females tended to begin spawning a year or so later than the males. The bimodal ages of males in Octoraro Creek were V and VI, 16% were VII, and one male was VIII. Females ranged from four to seven years old, with five and seven year olds each representing 43% of the sample population. The age

and size distribution of hickory shad populations in U.S. east coast river systems from Florida to North Carolina ranged from two to eight years and 216-487 mm FL.¹²⁴ Females tend to be larger at age than males.⁷³

In general, repeat spawning appears to be common in hickory shad runs; but it is also variable among river systems and can range from < 10% to over 80%.^{63,93,122,124} Schaeffer's¹²⁶ sample of hickory shad from Octoraro Creek, Maryland, showed that all fish spawned every year. Most of the females he examined were on their third spawning run; the males were about evenly divided between their fourth and fifth runs. One female was on her fifth run and one male was on his seventh. In Georgia streams, individual hickory shad can make at least one and commonly up to three to four spawning runs. Pate¹¹⁹ observed that hickory shad in the Neuse River, North Carolina, normally make three spawning runs per lifetime, but some males make up to five runs.

Limited fecundity data are available for hickory shad. Two estimates of fecundity for hickory shad populations in Octoraro Creek, Maryland, were 476,236 and 488,867 eggs per female. Numbers of eggs per female can range from 43,556 in three-year old fish (325 mm) to 347,610 eggs in six-year old fish of 434 mm.¹¹⁹ Manooch⁹⁶ reported that a two-year old female can spawn 61,000 eggs, and a six-year old female more than 300,000. Street¹³⁸ estimated the fecundity of the Altamaha River, Georgia, population of hickory shad at 509,749 eggs per female.

Gonadal maturation in females is very rapid.⁹⁷ Adult collections were typically composed of all green (not ready for spawning) or all spent (fully spawned) females. The ovary of a single female collected during the spawning run contained groups of eggs in various stages of maturation. These observations suggest that ripe eggs are released in small numbers over a prolonged period rather than during a single brief spawning event.

After spawning, hickory shad return to oceanic waters where their distribution and movements are essentially unknown.^{122,138} Hickory shad occasionally are harvested during summer and fall along the southern New England coast.³ These observations suggest that hickory shad may migrate northward from the mid-Atlantic and southeast Atlantic spawning rivers in a pattern that is similar to the coastal migrations of American shad.³⁵

ECOLOGICAL ROLE

AMERICAN SHAD

Food Habits

Young American shad are opportunistic and size selective plankton feeders. Copepods, other crustaceans, zooplankters, chironomid larvae, and terrestrial insects are important food items for the young fish in fresh-

water.^{80,81,101,147} Juveniles occasionally consume small fish species such as striped anchovy, bay anchovy, and mosquitofish.^{58,153} In the ocean, copepods and mysids are primary foods for all size American shad.¹³⁰ Adults also consume ostracods, amphipods, isopods, insects, and small fishes.^{58,79}

Competition

Juvenile American shad often coexist with young blueback herring and alewife in the same freshwater nursery areas. Hence, opportunities exist for interspecific competition among these three alosids. Competition between juvenile American shad and juvenile alewife may be minimized by differences in diel activity patterns.¹²⁷ Competition between juvenile American shad and juvenile blueback herring may be minimized by differences in feeding habits.^{50,42}

Competition with gizzard shad in the Susquehanna River and upper Chesapeake Bay may have contributed to the decline of upper Bay stocks of American shad, or could be another factor that is delaying recovery of these stocks, but the meager evidence is circumstantial. The annual catch per effort of gizzard shad in the fish lift at Conowingo Dam on the Susquehanna River steadily increased from 1972 through at least 1981,¹³ a period of rapid decline for American shad in Maryland.¹³⁵

American eels prey upon American shad eggs and juveniles in freshwater, and striped bass prey on the juveniles.^{99,148} Commercial landings of bluefish, a potential predator of young American shad, were relatively high from 1972 through 1986.⁶⁵ Large bluefish were also very abundant in the Bay from May through mid-October during 1988. Predation on juvenile American shad by bluefish and other large predators (e.g., weakfish) is perhaps a minor factor that could be delaying the recovery of American shad stocks in the Chesapeake Bay. Subadult American shad have been found in seal stomachs.¹⁰⁹ The adults appear to have few predators other than man.¹³¹

HICKORY SHAD

We could find no information on the food habits of larval or juvenile hickory shad. The adults are primarily piscivorous but also consume squid, fish eggs, small crabs, and pelagic crustaceans.^{55,154} The adults apparently do not feed during their freshwater spawning migrations.¹¹⁹

We could find no information on competition or predation for hickory shad. Competition with gizzard shad in the Susquehanna River may have contributed to the decline of the hickory shad populations in the upper Chesapeake Bay, or is at least one factor that is delaying recovery of the stocks. The abundance of gizzard shad in the Conowingo Dam fish lift (Susquehanna River) steadily increased from 1972 through 1981,¹³ coincident with a period of rapid decline for hickory shad in Maryland. The

synchrony may be causative or coincidental - we do not know.

POPULATION STATUS AND TRENDS IN CHESAPEAKE BAY

AMERICAN SHAD

Historically, American shad was a major fishery resource all along the Atlantic seaboard. However, between 1897 and 1940, annual harvests declined from over 20×10^6 kg to about 5×10^6 kg.⁹⁹ Suspected causes of these coastwide declines include pollution and siltation of spawning rivers, overharvesting, and construction of dams which prevented access to several spawning areas.¹⁴⁸

Records of Commercial and Recreational Landings

The American shad fishery in the Chesapeake Bay steadily increased throughout the 1800's and reached prominence toward the end of the century.¹⁴⁸ Commercial landings in Maryland peaked in 1890 at 3.2×10^6 kg. In 1896, the Maryland portion of the Bay was the fourth largest producer of American shad in the U.S.⁹⁹ The Susquehanna River and the upper Bay region once had the largest populations of spawning American shad in Maryland.^{134,135} Commercial landings in Virginia peaked in 1897 at 5.2×10^6 kg.

Commercial landings and stock abundance have steadily declined in the Chesapeake Bay since the late 1890's. Maryland and Virginia continued intensive exploitation of American shad through the 1960's, even though the stocks were declining.⁷³ By 1979, commercial landings in Maryland and Virginia had decreased to 8.2×10^3 kg and 451.4×10^3 kg.¹²²

The history of the recreational fishery for American shad began in the 1880's, but this source of exploitation is not well documented.⁷³ There were no survey data collected which described the extent of the recreational fishery when American shad were abundant in the Chesapeake Bay. Limited recreational surveys and creel censuses began in the late 1950's in the Conowingo Dam area of the Susquehanna River.⁷³ In 1958 and 1960, about 15,000 and 13,000 American shad (about 27,000 and 24,000 kg) were caught by anglers in the Conowingo Dam tailrace.

In 1980, the commercial and recreational fisheries for American shad were closed in Maryland,¹³⁵ but not in Virginia. Reported annual landings of American shad in Virginia from 1980 to 1985 stabilized at relatively low levels and have ranged from 0.2×10^6 kg to 0.7×10^6 kg.⁷

Commercial landings are only a rough index of American shad abundance in Chesapeake Bay, but nevertheless are the primary source of information. Little is known about the trends in effort either directed at or incidental to the

commercial fishery for American shad.⁷³ If catchability increased as stock abundance declined, as Crecco and Savoy³⁰ observed, the American shad stock in the Chesapeake Bay actually may have been declining before the records of commercial landings declined.¹³⁵ Recreational catches of and fishing effort for American shad are not compiled in Maryland and Virginia, but both are probably small relative to commercial landings and effort. For additional information on the commercial and recreational fisheries for American shad in the Maryland portion of the Bay, see Krauthamer and Richkus.⁷³

Juvenile Abundance Indices

The relationship between numbers of juvenile American shad produced each year and parental stock size has been studied intensively in the Connecticut River.^{30,31} It was concluded that year-class strength was not related to stock size, but was regulated primarily by environmental factors, particularly river flow and temperature. Only recently have detailed life history and population dynamics studies been initiated in other Atlantic coast spawning rivers.¹²²

If American shad populations in Maryland likewise are influenced strongly by environmental factors, the declining trend in juvenile abundance indices for 1958 through 1984 (juvenile finfish seine survey¹³⁵) suggests that environmental conditions were periodically unfavorable through the early 1970's, and have been consistently unfavorable since. Unfortunately, the degree to which the seining sites, selected to provide striped bass monitoring information, are representative of the American shad nursery habitat has not been established.⁷³

Current population levels of American shad are very low in Maryland, and perhaps near or below the critical threshold for a viable spawning stock size. Year class success should be most dependent upon environmental conditions when spawning stocks are large, and upon spawning stock size when spawning stocks are depressed. Therefore, parental stock size may be playing a much larger role in juvenile production in Maryland rivers, compared to Virginia rivers, the Connecticut River or the Hudson River, where American shad stocks are more abundant.¹²²

Methods used in Virginia's juvenile American shad survey have changed over the years, so only a limited time series is comparable to the Maryland survey.¹³⁵ In two Virginia rivers, the Mattaponi and Pamunkey, juvenile abundance indices were relatively stable between 1980 and 1987.⁶

Current Status of Spawning Populations in Major Bay Tributaries

A qualitative assessment of the current status of American shad spawning populations in each of the major river systems in Chesapeake Bay is presented in this section.

AMERICAN SHAD AND HICKORY SHAD

Another recent assessment carried out independently by Richkus *et al.*¹²³ reached similar conclusions and generally confirmed our observations.

Our assessment was drawn from recent survey data, the observations of fisheries biologists associated with those surveys, and other informed individuals,^{6,7,60,86,87,88,89,91,92,114,149,150} and personal communications (James Mowrer, Jay O'Dell, Harley Speir, and James Uphoff, Maryland Department of Natural Resources; Herb Benjamin, Northeast, Maryland; Joice Davis, Joseph Loesch, and James Owens, Virginia Institute of Marine Science). This assessment is relevant to the 1980's, especially the latter half of the decade, and represents a perspective on the current spawning populations compared to conditions in the late 1960's and early 1970's when Baywide American shad populations were much more abundant than they are today.

Susquehanna River and upper Chesapeake Bay

The population is at a very low level of abundance, but appeared to increase about 28-fold between 1980 (population estimate of 2,675 adults) and 1989 (population estimate of 75,329 adults). In 1989, catch per effort values for juvenile American shad in haul seines (0.17 fish per haul) and trawls (0.57 fish per trawl) in the upper Bay were the highest abundance indices recorded since 1980.

Patuxent River

A remnant population that is at a very low level of abundance and may be declining.

Potomac River

A remnant population that is at a low level of abundance.

Rappahannock River

The population is at a very low level of abundance and appears to be declining.

York River

The population is at a low level of abundance and appears to be stable. Since 1980, annual juvenile densities were higher in the Mattaponi River than the Pamunkey River by an average factor of about four.

James River

The population is at a low level of abundance and appears to be declining.

Chickahominy River

Current status is not known, but the population is probably at a very low level of abundance. There has been no commercial fishery for American shad since the late 1960's.

Pocomoke River

A remnant population that is at a very low level of abundance but appears to be increasing.

Wicomico River

A remnant population that is at a very low level of abundance and appears to be declining.

Nanticoke River

The population is at a low level of abundance but appears to be stable.

Choptank River

A remnant population that is at a very low level of abundance.

Chester River

Probably no spawning run left.

Sassafras River

Probably no spawning run left.

Bobemia River

Probably no spawning run left.

Elk River - Chesapeake and Delaware Canal

A remnant population that is at a low level of abundance but may be increasing.

Northeast River

Probably no spawning run left.

HICKORY SHAD

Hickory shad never have been as abundant as other alosids in Chesapeake Bay,⁶⁵ probably because they are near the northern limits of their spawning range.^{2,135} Hickory shad are of minor importance as a foodfish because the meat is bony and considered inferior to the larger American shad. However, hickory shad roe is considered by some to be superior to American shad roe.² Hickory shad are a desirable sport fish during the spawning run.^{65,126}

Records of Commercial and Recreational Landings

Hickory shad frequently are misidentified and taken as by-catch in commercial fisheries directed at the larger American shad.¹²² Therefore, records of commercial landings may underestimate actual landings and offer an inaccurate profile of hickory shad population status and trends. Little is known about trends in fishing effort in Maryland directed at or incidental to the commercial fishery for hickory shad.⁷³ In Maryland, records of commercial landings available from 1959 through 1979 ranged from a high of 20,955 kg in 1970 to a low of 368 kg in 1977.¹²² In January 1981, the catch of hickory shad in

Maryland was prohibited and the commercial and recreational fisheries have remained closed.⁶⁵

In Virginia, records of commercial landings for 1920 to 1981 ranged from a peak of 106,171 kg in 1925 to a low of 629 kg in 1977.² Since 1977, the reported landings of hickory shad in Virginia have remained fairly stable near the low catch of 1977.⁶⁵ Commercial and recreational fishing for hickory shad in Virginia currently is not prohibited.

Directed fisheries for hickory shad in Chesapeake Bay during the 1960's and 1970's were limited to a few early spring gill netters and pound netters, and spotty spring recreational fisheries in several streams prior to the spawning migrations of the more abundant American shad and river herrings.^{2,13,135} Sport fishermen take hickory shad by casting shad darts, spoons, and spinners in non-tidal reaches near the spawning grounds.⁷⁴ Limited recreational surveys and creel censuses concentrated in the Conowingo Dam vicinity of the Susquehanna River, Maryland, began in the late 1950's.⁷³ In 1958, the recreational fishery in this area caught and reported 2,755 hickory shad (about 5,000 kg). In 1960, anglers caught about 4,000 hickory shad (about 5,400 kg) in Octoraro and Deer Creeks, both tributaries to the lower Susquehanna River in Maryland.

Collections of adult hickory shad during spring 1975 and 1976 in Octoraro Creek, Maryland¹²⁶ showed an abnormal age distribution skewed toward the older age groups: 91% of the collections were comprised of age V or older fish. Year class contributions showed evidence of a decline since 1970, with no recruitment to the population spawning in Octoraro Creek since 1972. Schaeffer¹²⁶ concluded that the hickory shad spawning runs into the Susquehanna River, Deer Creek, and Octoraro Creek noticeably declined beginning about 1973. Additional observations which supported the evidence for this period of decline were reported by Krauthamer and Richkus.⁷³ Numbers of hickory shad taken by hook and line in Deer Creek, Octoraro Creek, and Northeast Creek apparently increased from essentially none in the early 1980's to a few by the late 1980's (personal communication: Herb Benjamin, Herb's Tackle Shop, Northeast, Maryland).

Juvenile Abundance Indices

We could find no information on annual abundance trends for juvenile hickory shad in Maryland or Virginia tributaries to Chesapeake Bay. Very few juveniles were taken in Maryland's Baywide seine survey (e.g., 2 in 1961, 2 in 1969, and 1 in 1971).⁷³

Current Status of Spawning Populations in Major Bay Tributaries

Hickory shad either have been collected or authoritatively reported to occur throughout the Maryland portion of

Chesapeake Bay.⁹⁷ However, little information is available on the specific distributions of the early life stages in Maryland tributaries or in the James, Pamunkey, Mattaponi, York, Rappahannock, and Potomac Rivers of Virginia.³⁹ The available information indicates that hickory shad spawning populations in Chesapeake Bay are now at very low levels of abundance in a few tributaries and probably non-existent in most others.

A single running-ripe (or spawnable) female and several running-ripe males were collected on May 10, 1956 in a tidal fresh area of the upper Patuxent River near Queen Annes Bridge in Anne Arundel County, Maryland.⁹⁷ Adult hickory shad were collected at this spawning location from about mid-April (mean river temperature = 12°C) through early June (mean river temperature = 18°C). The same section of the Patuxent River was sampled with seines in spring 1975, but no hickory shad were collected.¹²⁶ Local residents and fishermen reported that hickory shad had been rare in that section of the Patuxent River since about 1970. In 1955, many adult hickory shad were examined from catches of anglers and netters in the Patuxent, Choptank, and Northeast rivers, Maryland; but only green roe (ova not yet ovulated) and spent (spawned-out) individuals were found.⁹⁷ In spring 1975 and 1976, Schaeffer¹²⁶ sampled Octoraro Creek, near the Rowlandsville Bridge, a tributary to the Susquehanna River in Cecil County, Maryland. He collected 71 adults (63 males and 8 females) for age and growth examinations. Octoraro Creek was a popular sport fishing area for hickory shad during the spawning run prior to closure of the fishery in Maryland in 1981.⁷³

Transforming young hickory shad (9-20 mm TL) were tentatively identified by Mansueti⁹⁷ from plankton samples collected on May 7, 1954 in the upper Patuxent River estuary near Lower Marlboro, Maryland, in slightly brackish water, about 9 km downstream from a known spawning location. During an eight year seine survey of young fishes in the Patuxent River (1950-1958) from June through October, only a few dozen hickory shad juveniles were collected while several thousand of the other three alosid species were captured.⁹⁷ The sparse data suggest that most juvenile hickory shad emigrate from the spawning rivers and estuaries in early summer, before the juveniles of the other three species of alosids leave.

Lippson *et al.*⁸³ speculated that the distribution of hickory shad in the Potomac River approximates that of American shad. Their Folio Maps 7 and 8 show that hickory shad spawn from late April through May, mostly in the tidal freshwater mainstem of the Potomac River on open water shoals. Some spawning also may occur in slightly brackish areas (0-3 ppt salinity) and in the lower portions of some tributaries such as St. Clements Bay (St. Mary's County), Nanjemoy Creek (Charles County), and Broad Creek (Prince Georges County). Adult hickory shad may lag

slightly behind adult American shad in leaving the Potomac River and returning to the Atlantic Ocean after spawning.

The current distribution of hickory shad spawning in Maryland waters of Chesapeake Bay is largely unknown, presumably due to their very low abundance and the relative lack of interest in hickory shad compared to the other alosids. Surveys of fish eggs and larvae in the Patuxent River (1963-1965) and in the upper Bay (1966 and 1967) failed to collect any hickory shad eggs or larvae.⁴⁴ One egg was collected in the Magothy River in 1965. O'Dell *et al.*¹¹³ did not collect any hickory shad adults or eggs during a 1970-1971 survey of the Potomac River drainage system. They did collect a few hickory shad larvae in the Wicomico River, Charles County (at the mouth of Allen's Fresh Run) and in Broad Creek. They also described hickory shad larvae as "being of probable occurrence" in Nanjemoy, Mattawoman, Pamunkey, and Piscataway creeks.

No evidence of hickory shad spawning was documented in the mainstem Patuxent River and 58 tributaries between 1980 and 1983.¹¹⁴ The section of the upper Patuxent River from Queen Anne Bridge upriver to U.S. Route 50 was the site of an active sport fishery for hickory shad until about 1970.

No hickory shad were collected during 1984 and 1985 in the mainstem Choptank River and 13 tributaries.¹⁵⁰ No hickory shad were collected during 1985 juvenile alosid surveys in the Chester, Choptank, Nanticoke, Pocomoke, and Patuxent rivers, and in the upper Bay region.⁶⁰ Hickory shad eggs were collected from one Maryland Department of Natural Resources (MDNR) sampling site in the Wicomico River (Eastern Shore) at river mile 13.3 in spring 1986.¹⁴⁹

Juveniles were collected at Mill Pond (Chester River) and Middle River in the upper Bay region.⁷³ Anecdotal information suggests that some adult hickory shad occasionally still are being caught (and presumably released) by sport fishermen in a few upper Bay tributaries: Deer, Octoraro, and Northeast creeks (personal communications: Harley Speir, MDNR, and Herb Benjamin, Herb's Tackle Shop, Northeast, Maryland). The MDNR alosid surveys during the 1980's offer only a few insights into the distribution of hickory shad spawning populations in Maryland, and support the perspective that hickory shad stocks are at very low abundance levels.

The current distribution of hickory shad spawning populations in Virginia waters is not much more certain. Two recent reports described the results of surveys of tributaries in the lower James River¹¹⁵ and the middle James River¹¹⁶ for spawning use by striped bass and anadromous alosids. Barriers to upstream movements of

migratory fish also were identified in each tributary. Hickory shad were not mentioned. The same survey approach was extended to 148 Virginia tributaries of the lower Potomac River downstream of Great Falls.¹¹⁷ The report concluded that anadromous alosids do not spawn in any tributaries downstream from Popes Creek (river mile 38). The authors did not mention the current use of any surveyed tributary by hickory shad.

Our review of several annual reports of *Alosa* stock composition and year-class strength in Virginia compiled from 1976 to 1988^{6,7,84,86,87,88,89,91,92,93,94} did not find mention of any adult juvenile hickory shad collections in the James, Appomattox, Chickahominy, York, Pamunkey, Mattaponi, Rappahannock, or Potomac rivers. The consensus among fisheries workers at the Virginia Institute of Marine Science (VIMS) is that remnant populations of hickory shad probably still spawn in the Rappahannock and York River systems, but in such low numbers that juveniles have not been collected in push net or trawl surveys conducted since the early to mid-1970's (personal communications: Joseph Loesch, Joice Davis and James Owens, VIMS). Their views are based on scattered reports of hickory shad catches during the 1980's by sport fishermen and commercial gill netters operating near Tappahannock, on the Rappahannock River, and by commercial gill netters operating near West Point, on the York River at the confluence of the Mattaponi and Pamunkey rivers.

HABITAT REQUIREMENTS

AMERICAN SHAD Temperature

Suitable water temperatures for the development and survival of American shad eggs range from 13-26°C.^{137,95} The optimum temperature for egg development is about 17°C.⁸⁰ Temperatures below 8-10°C and above 27°C are unsuitable because embryo development either ceases or abnormalities appear in the resulting larvae. No viable larvae developed from eggs incubated in water temperatures above 29°C.⁸ Abnormalities also may occur if egg incubation temperatures rise to 22°C.⁸⁰

American shad eggs can tolerate extreme temperature changes if exposure durations are relatively short. Schubel and Auld¹²⁹ simulated the time-temperature exposure conditions associated with cooling water condenser systems of steam-electric generating stations. Eggs were exposed to temperatures from 22.5-24°C for 5-25 minutes, and then cooled to ambient temperatures over 1-3 h. Eggs acclimated at 18.5°C exhibited no significant hatching differences between the control and treatment groups. A similar experiment exposed eggs to temperatures from 22.5-26.5°C for 2.5-60 minutes.¹²⁸ Eggs acclimated at 16.5°C showed no significant differences in hatching success among the various time-temperature treatments.

American shad eggs were acclimated at 17–24°C and then exposed to temperature increases of 10–14.5°C for 2.5–60 minutes.⁶⁹ Temperatures $\geq 34.0^\circ\text{C}$ were lethal to eggs; lower temperatures produced variable results. Similar results were reported for eggs acclimated to 20.5°C and exposed to temperatures in excess of 35°C.¹³⁰ American shad eggs acclimated at 20.5°C could tolerate a 30 minute exposure to 30.5°C. However, the eggs could tolerate only a five minute exposure at 35.2°C. Koo *et al.*⁷² and Koo⁷⁰ also reported an upper incipient lethal temperature of 32.5°C for American shad eggs after a 15 minute exposure. Sensitivity to temperature decreased as egg development increased.⁷¹ Younger eggs (gastrula stage) were significantly more sensitive to 29.5°C than the older stages (tail-free embryo), which could tolerate 31.5°C.

Maximum survival of American shad larvae occurs between 15.5–26.5°C.⁶⁴ Koo *et al.*⁷¹ and Koo⁷⁰ reported that larvae acclimated to 20.5°C survived a brief (15 minute) exposure to 31.5°C, but suffered significantly greater mortality when exposed to 33.5°C.

A habitat suitability index for American shad indicated that the optimum-temperature range for juveniles is 15.6–23.9°C.²⁸ Larvae and juveniles were collected when temperatures were between 10–25°C in the upper Chesapeake Bay; 93% were collected at 21°C.⁴⁴ Juvenile American shad can detect and avoid rapid temperature increases in excess of 4°C above ambient (24–28°C).¹¹¹ Juveniles should be able to avoid potentially upper lethal temperatures during migration from nursery areas. Young American shad avoided effluent temperatures greater than 30°C by swimming below the power plant outflow.¹⁰¹ The natural upper temperature limit for juveniles is near 30°C. A 96 h TL₅₀ (lethal temperature that killed 50% of the test organisms) of 31.6°C was reported for young American shad acclimated to 24°C.⁴⁵

A series of temperature avoidance studies with juvenile American shad was summarized in a power plant annual operating report.¹²¹ Individuals acclimated to 28°C avoided temperatures ranging from 32–34°C. A critical thermal maximum of 34–35°C was reported for juvenile American shad in the Neuse River, North Carolina.⁵⁹

The effects of decreasing temperatures on juvenile American shad, acclimated to 24°C, was examined by Chittenden.²¹ He concluded that the lower lethal temperature was 2.2°C. Survival was limited after extended exposure to 4–6°C. In other studies of the effects of temperature decreases,¹²¹ juveniles acclimated to 25°C suffered 100% mortality when the temperature was decreased to 15°C. No survival was recorded for juveniles acclimated to 15°C and exposed to temperatures $\leq 5^\circ\text{C}$. Individuals acclimated to 5°C and then exposed to 1°C also experienced 100% mortality.

The effects of heated effluents on juvenile American shad were examined by Marcy *et al.*¹⁰² in an in-situ experiment. A live-box containing the test organisms was drifted through the heated effluent of a power plant on the Connecticut River. The following behavioral changes in response to heated effluent were observed: (a) schooling was not observed at ambient temperatures (19°C); (b) the juveniles formed a tight school immediately upon entering the heated effluent; (c) the juveniles began swimming rapidly in a circular pattern and then dispersed into smaller schools after one minute of exposure to 30°C; (d) disorientation and small school disintegration occurred after two minutes of exposure to 31.2°C; (e) no evidence of schooling and continued disorientation associated with loss of equilibrium occurred after 3–4 minutes of exposure to 31.8°C; and (f) total mortality occurred within 4–6 minutes of exposure to 32.2°C. This upper lethal temperature is similar to that reported in laboratory studies^{111,121}. Underwater observations during submerged cage tests indicated that the juveniles avoided effluent temperatures greater than 30°C. The investigators concluded that 30°C was the upper natural temperature limit.

Salinity

American shad eggs were collected in areas of the upper Chesapeake Bay with 0–1 ppt salinity.⁴⁴ Eggs and larvae can survive exposures to salinities ranging from 7.5–15 ppt at 12 and 17°C.⁸⁰ Survival at 15 ppt was greater at 17 than at 12°C. Young American shad appear to be very tolerant of a wide range of salinities, and this tolerance begins early in life.²⁰

Larval and juvenile American shad were collected only in freshwater areas in the upper Chesapeake Bay.⁴⁴ Chittenden²³ examined the effects of rapid and gradual (six day) changes between salt water and fresh water on juveniles held at 17°C. No mortality was observed when juveniles were abruptly or gradually transferred from fresh water or 5 ppt to 30 ppt. These results are similar to those Chittenden²² reported for salinity transfer experiments conducted with blueback herring. Conversely, 100% mortality occurred within 9–19 h when juvenile American shad were transferred directly from 30 ppt salinity to fresh water. No mortality was observed when juveniles were moved directly from 5 ppt to fresh water.²³ Ions in salt water apparently act as buffers to reduce the Bohr effect, thereby increasing the handling success with American shad in salt water compared to fresh water.

Given their anadromous life history, adult American shad should also exhibit a wide range of salinity tolerance. Dodson *et al.*⁴¹ examined the effects of salinity on adults by observing their movements with ultrasonic tracking techniques. They reported that a 24–53 h period within the saltwater-freshwater interface zone was necessary for the adults to make physiological adjustments successfully during spawning runs from salt water to fresh water.

Significant mortality of adult American shad that began five hours after a transfer from salt water (28 ppt) to fresh water, accompanied by a 5–6°C temperature increase, was reported by Leggett and O'Boyle.⁷⁸ Changes in several blood chemistry parameters were also noted.

Temperature and Salinity

The tolerance of juvenile and adult American shad to rapid temperature and salinity changes was examined by Tagatz.¹⁴² The juveniles generally could cope with abrupt transfers from salt water to fresh water, but had difficulty adapting to transfers from fresh water to salt water. No mortality was observed when juveniles were abruptly transferred from salt water (15 and 33 ppt salinity) to fresh water, in association with temperature increases < 14 °C. Conversely, 100% mortality (no survival) was observed when juveniles were transferred from fresh water (at 21.1°C) to salt water (33 ppt) at 7.2–12.8°C. Survival varied from 30–50% after two days when juveniles were transferred from fresh water to 15 ppt in association with a temperature decrease < 4 °C. Mortality was 60% after 48 h when juveniles were transferred directly from fresh water to 33 ppt at 21.1°C.

A discrepancy in juvenile survival was noted between the data of Tagatz¹⁴² and Chittenden.²³ Chittenden²³ reported no mortality after 16 days when juveniles were transferred abruptly from 0 to 30 ppt at 17°C, whereas Tagatz¹⁴² reported 60% mortality after two days when juveniles were abruptly transferred from 0 to 30 ppt at 21.1°C.

Adult American shad were tolerant of rapid changes from fresh water to salt water (23–24 ppt) during a temperature change ≤ 9°C, but they did not survive rapid changes from salt water (27 ppt) to fresh water during a 14°C temperature increase. Mortality of adults varied from 0–40% during direct transfers from salt water (13–25 ppt) to fresh water in association with temperature increases ≤ 5.6°C.

Dissolved Oxygen

Lethal dose (LD₅₀) values for dissolved oxygen (DO) ranged from 2.0–2.5 mgL⁻¹ for Connecticut River American shad eggs, and were close to 3.5 mgL⁻¹ for Columbia River eggs.⁸ The LD₅₀ values were based on the percentage of crippled or abnormal larvae that hatched from eggs incubated at several DO concentrations. A good hatch with a high percentage of normal larvae required DO levels during egg incubation of at least 4.0 mgL⁻¹. No eggs survived DO levels of 1.0 mgL⁻¹. No American shad eggs were collected in the Connecticut River when DO concentrations were less than 5 mgL⁻¹.¹⁰¹ Eggs were collected in the Neuse River, North Carolina, within a DO range of 6–10 mgL⁻¹.⁵⁴ I could find no information on DO optima or tolerances for American shad larvae.

Juvenile and adult American shad require relatively well-oxygenated waters. Dissolved oxygen concentrations less

than 5.0 mgL⁻¹ should be considered sublethal to juveniles and adults.¹¹⁰ Concentrations of DO less than 3.0 mgL⁻¹ blocked adult and juvenile migrations, and concentrations less than 2.0 mgL⁻¹ were lethal. For migrating adults and juveniles, DO must be at least 4 to 5 mgL⁻¹ in headponds above hydroelectric dams on the St. John River, New Brunswick.⁶² Healthy-appearing juveniles were collected in the Hudson River, New York, where DO was 4 to 5 mgL⁻¹.¹⁰

In the laboratory, DO less than 5 mgL⁻¹ was lethal to juvenile American shad;⁴⁶ however, Chittenden²⁴ believed these findings were biased by handling stress. Chittenden's studies^{20,24} showed that juvenile American shad did not lose equilibrium until DO decreased to 2.5–3.5 mgL⁻¹; mortality increased at DO below 2 mgL⁻¹, and all fish died when DO declined to 0.6 mgL⁻¹. Minimum daily DO levels of 2.5–3.0 mgL⁻¹ should permit American shad to migrate through polluted areas, but 4.0 mgL⁻¹ appears to be needed in spawning areas.²⁴ These conclusions are supported by recent observations of increased spawning of American shad in the Delaware River coincident with improved DO concentrations in the tidal portion.¹⁰⁵

No mortality was observed when juvenile American shad were exposed for 96 h to DO concentrations between 2–4 mgL⁻¹, but respiratory movements increased when DO fell below 4 mgL⁻¹.¹⁴³ Dorfman and Westman⁴³ reported that juveniles could survive brief (5 minute) exposures to DO concentrations as low as 0.5 mgL⁻¹ (at 17.8°C), if DO greater than 3 mgL⁻¹ was readily available to the test organisms. The juveniles apparently could not detect and quickly avoid the low DO concentrations.

pH

A paucity of information exists concerning the effects of pH on various life stages of American shad.⁶⁶ In a laboratory study, Bradford *et al.*⁸ reported that fertilized eggs developed successfully between pH 5.5 and 9.5 at 18 to 19°C, but most eggs succumbed to pH below 5.2 (0–32% hatch). The calculated lethal dose to 50% of the eggs (LD₅₀) exposed to pH 3.0–6.0 treatments was about pH 5.5; however, many of the larvae that hatched at pH 5.5 were deformed. A suitable pH for American shad eggs was ≥ pH 6.0. In another laboratory study, Klauda and Palmer⁶⁷ reported that advanced embryos (24 h post-fertilization) could tolerate pH 5.7, 6.7 and 7.5 treatments, but not pH 5.0 treatments, with no aluminum present. Simultaneous exposure to acidic pH and a range of dissolved aluminum concentrations (50–400 µg/L) increased egg mortality rates in the pH 5.7 treatment to 84%.

Yolk-sac larvae also were exposed to four pH levels (5.7, 6.2, 6.7, 7.5) and four dissolved aluminum concentrations (50, 100, 200, 400 µg/L) in the same laboratory study.⁶⁷ The larvae could tolerate acid-only treatments of pH 6.7

and 7.5, but mortality was 100% in the pH 5.7 and 6.2 treatments after only a 55 h exposure. Simultaneous exposure to the lowest concentration of aluminum ($50 \mu\text{gL}^{-1}$) reduced survival of the larvae in each pH treatment.

The effects of acid pulses on pre-feeding and feeding American shad larvae also were examined in the laboratory.⁶⁸ Feeding larvae were more sensitive than pre-feeding larvae to single acidic pulses (pH 7.6-6.2; pH 7.6-5.2), with or without a concomitant aluminum pulse ($32\text{--}104 \mu\text{gL}^{-1}$). A conservative critical acidity condition for American shad reproduction in the Chesapeake Bay was defined by Klauda⁶⁶ as an acidic pulse from circumneutral to pH between 6.2-6.7 associated with a total monomeric aluminum peak of at least $30 \mu\text{gL}^{-1}$ that lasted for at least 48 hours.

We could find no information on pH optima or tolerances for juvenile, subadult, or adult American shad.

Hardness and Alkalinity

We could find no information on water hardness optima or tolerances for any life history stage of American shad. Their wide salinity tolerance range (see **Salinity** section above) suggests that hardness is not likely to be a critical habitat requirement.

We could find no information on alkalinity optima or tolerances for any life history stage of American shad. However, since the larvae appear to be quite sensitive to moderate acidity (see **pH** section above), reproductive success in poorly buffered (low alkalinity) spawning and nursery areas that are subjected to episodic or chronic acidity inputs may be reduced compared to success in river systems with higher alkalinities that are less vulnerable to acidification.

Suspended Solids

American shad larvae appear to be more sensitive to elevated levels of suspended solids than other early life history stages. Suspended solids concentrations $\leq 1000 \text{ mgL}^{-1}$ did not significantly reduce the hatching success of eggs.⁴ However, four-day exposures of yolk-sac larvae to suspended solids concentrations $\geq 100 \text{ mgL}^{-1}$ significantly reduced larval survival relative to the controls.

Extensive dredging of the Hudson River produced no measurable adverse effects on American shad abundance compared to other population stressors such as commercial fishing.¹⁴⁴ Adults readily migrate into the Shubenacadie River, Nova Scotia, where suspended solids concentrations were sometimes as high as 1000 mgL^{-1} .⁸⁰ High turbidity (Secchi disk mean = 0.30 m) in the inner Bay of Fundy, Canada, may restrict light penetration and provide the filter-feeding and planktivorous American shad with a competitive advantage over other large pelagic fishes

that apparently cannot feed effectively in these turbid conditions.³⁴

Current Velocity and Turbulence

Optimal water velocities for American shad spawning habitats and egg incubation success range from about $30\text{--}90 \text{ cm s}^{-1}$.¹³⁷ This velocity range was based on field observations reported by Walburg and Nichols¹⁴⁸ and Kuzmekus.⁷⁵ Optimal current velocities for larvae and juveniles probably range from about $6\text{--}30 \text{ cm s}^{-1}$ and from about $6\text{--}75 \text{ cm s}^{-1}$, respectively.

We could find no information on current velocity or turbulence tolerances for any life history stage of American shad. Velocity and turbulence-related stresses encountered by American shad that pass through turbines at hydroelectric stations could provide some insights to their responses to these extreme conditions.⁴⁸

Physical Habitat

Substrate type should be relatively unimportant to successful American shad spawning since the eggs are broadcast into the water column over a range of substrates and most are carried downstream.^{95,99} Only in areas where the eggs settled to the bottom, were covered by silt or sand and then smothered would substrate become a critical habitat problem. American shad also show little depth preference for egg deposition and spawn at depths ranging from 0.45-7 m.⁹⁵ Stier and Crance¹³⁷ suggested that at least 50% of the estuarine habitat used by American shad should be subtidal.

HICKORY SHAD

Our review of the literature revealed that information on the habitat requirements for hickory shad is sparse and limited to the material presented below. Hickory shad are closely related to American shad and the two river herrings; therefore it is reasonable, given current data limitations, to assume that hickory shad requirements are similar to the other three alosids.^{65,16}

Temperature

Hickory shad eggs have been collected in water temperatures ranging from $9.5\text{--}22^\circ\text{C}$.^{9,54,103,119,138,139} Eggs hatch in 48-72 hours when incubated in the laboratory at temperatures between $21\text{--}18^\circ\text{C}$.⁹⁷ We could find no information on temperature optima or tolerances for any life history stage of hickory shad.

Dissolved Oxygen

Live hickory shad eggs were collected in areas of the Neuse River, North Carolina, where DO ranged from $5\text{--}10 \text{ mgL}^{-1}$.⁵⁴ We could find no information on dissolved oxygen optima or tolerances for any life history stage of hickory shad.

Salinity

Juvenile hickory shad were collected during summer in estuarine sections of the Altamaha River, Georgia, where salinities reached 10 ppt.¹³⁸ In August and December, they were captured in salinities ranging from 10-20 ppt. Adults were collected in salinities ranging from 2.0-10.7 ppt in the St. Johns River, Florida.¹⁰⁶ We could find no information on salinity optima or tolerances for any life history stage of hickory shad. Since hickory shad are anadromous and spawn in mostly freshwater areas, salinity tolerance data for eggs and larvae would be most useful for evaluating habitat requirements.

pH

Live hickory shad eggs were collected in areas of the Neuse River, North Carolina, where pH ranged from 6.4-6.5.⁵⁴ We could find no information on pH optima or tolerances for any life history stage of hickory shad. Because the older juveniles, subadults and adults occur primarily in well-buffered estuarine and marine habitats, pH tolerance data for the eggs and larvae would be most useful for evaluating habitat requirements.

Hardness and Alkalinity

We could find no information on hardness or alkalinity optima or tolerance for any life history stage of hickory shad.

Suspended Solids

We could find no information on suspended solids optima or tolerances for any life history stage of hickory shad.

Current Velocity and Turbulence

We could find no information on swimming ability and current velocity or turbulence optima or tolerances for any life history stage of hickory shad.

Physical Habitat

Adult hickory shad appear to spawn in a diversity of physical habitats ranging from backwaters and sloughs, to tributaries, to mainstem portions of large rivers in tidal and non-tidal freshwater areas. We could find no information on specific physical habitat optima and tolerances for other life history stages of hickory shad.

SPECIAL PROBLEMS

AMERICAN SHAD

Contaminants

Relatively little information exists on the acute and chronic effects of contaminants on various life history stages of American shad.

The lethal dose (LD₅₀) for sulfates to eggs was > 1000 mgL⁻¹ at 15.5°C.⁸ The LD₅₀ for iron to eggs was greater than 40 mgL⁻¹ over a pH range from 5.5-7.2.⁸ Eggs exposed to zinc and lead concentrations of 0.03 and 0.01 mgL⁻¹ ex-

hibited very high mortality within 36 h of exposure.¹⁰⁷ Low hardness of the test water (12 mgL⁻¹) apparently intensified the toxicity of these two metals to American shad eggs. Available information on aluminum toxicity to eggs and yolk-sac larvae was discussed above in the pH section.

Juvenile American shad avoided a total residual chlorine concentration of 0.07 mgL⁻¹ when tested in 7 ppt salinity at 19°C.¹²¹

Tagatz¹⁴³ reported 48 h lethal concentrations (LC₅₀) for juveniles ranging from 2,417-91,167 mgL⁻¹ for gasoline, No. 2 diesel fuel and bunker oil. The toxicity of gasoline and diesel fuel to juvenile American shad increased when DO was simultaneously reduced. Exposure of juveniles to gasoline concentrations of 68 mgL⁻¹ at temperatures of 21-23°C resulted in a lethal time (LT₅₀) of 50 minutes when DO was reduced to 2.6-3.2 mgL⁻¹. An LT₅₀ of 270 minutes was reported when juveniles were exposed to 84 mgL⁻¹ of diesel fuel at temperatures of 21-23°C and DO between 1.9-3.1 mgL⁻¹.

Nutrients

We could find no information which would directly implicate high nutrient levels as a factor which has contributed to the Bay-wide decline of American shad populations in Chesapeake Bay. The rapid decline in American shad runs in the Delaware River during the early 1900's was attributed to severely depressed DO in the tidal river between Wilmington and Philadelphia.^{20,46,110} The poor water quality apparently blocked a portion of the adult population during their spring upstream migration to spawning areas, and prevented most of the juvenile population from emigrating seaward in the fall. American shad spawning has increased in the Delaware River since 1981, presumably because of improved DO in the tidal areas.¹⁰⁵ Rulifson *et al.*¹²⁴ mentioned low DO, sewage outfalls, and poor water quality as nutrient-related factors that were "possibly important or very important in contributing to the decline of certain populations of American shad" in North Carolina, South Carolina, Georgia and Florida.

Nutrient inputs to Chesapeake Bay and its tributaries from point sources, stormwater runoff and atmospheric deposition are of concern to scientists and resource managers. Excessive nutrient enrichment stimulates heavy growth of phytoplankton. Decay of phytoplankton blooms involve high rates of oxygen consumption which can lead to low DO during the growing season in the bottom waters of the Bay's deeper channels, and to diurnally low DO in tidal tributaries.^{27,145} These conditions can stimulate fish kills during hot summer months. Nutrient reduction is a major goal of the 1985 Chesapeake Bay Restoration and Protection Plan.^{33,136}

Parasites and Diseases

American shad seem to be relatively free of parasites.¹³¹ Parasites that have been reported include nematodes, trematodes, round worms, sea lice, acanthocephalans, sea lamprey, and freshwater lamprey.¹⁴⁸ A bacterium, *Aeromonas liquefaciens*, was the lethal agent in an American shad kill in California.⁵¹ However, stress induced by low DO ($< 3 \text{ mgL}^{-1}$) probably triggered the epidemic.

Impediments to Spawning Migrations

Dams built during the 1800's and in the early to mid-1900's on several major tributaries to Chesapeake Bay have reduced substantially the amount of spawning habitat available to American shad^{2,17} and likely contributed to long-term stock declines.⁹⁹ Construction of the Conowingo hydroelectric power dam at river mile 10 in 1928 blocked all but about 16 km of the Susquehanna River to American shad spawning migrations. The Conowingo Dam was the fourth in a series of dams that was constructed between 1901 and 1928.¹¹ The other three dams were built at river mile 55 (York Haven), at river mile 34 (Safe Harbor), and at river mile 26 (Holtwood). Before the York Haven and Holtwood Dams were constructed between 1904 and 1916, American shad could migrate upriver at least as far as Binghamton, New York (river mile 330) to spawn.¹⁵¹

A major program is underway in the Susquehanna River which involves the U.S. Fish and Wildlife Service, New York Department of Environmental Conservation, Pennsylvania Fish Commission, MDNR, and five electric utilities. The multi-year program began in 1980 and seeks to restore American shad to the river.^{17,72,135,140,141} The goal of the restoration program is to establish a run of 2,000,000 American shad through use of hatcheries, transplanting gravid adults, and construction of fish passage facilities.

A second permanent fish passage facility designed for the Conowingo Dam began operation in spring 1991 at a cost of \$12.5 million.¹⁸ This facility will supplement the existing fish lift which has operated since 1972. Design planning for fishways at the Holtwood, Safe Harbor, and York Haven dams on the Susquehanna River is in progress.

The Conowingo Dam may have played two additional roles in the decline of the Susquehanna River American shad stock. The effect of flow alterations at the hydroelectric facility is one major issue that has been raised.⁷³ Another issue relates to the impoundment of water behind the dam during low flow periods in summer and fall, which leads to the discharge of water with very low DO to downstream areas.

The migration of American shad up the Potomac River essentially is blocked by Little Falls Dam at river mile 117, about 2 km upstream from Washington, D.C.¹¹³ This dam

has excluded American shad from about 15 km of potential spawning habitat since the early 1950's.¹⁷ Discussions among officials from the District of Columbia, Virginia, Maryland, Army Corps of Engineers, and interested federal agencies have suggested several mitigative options: (a) a new fishway could be constructed on the Virginia side of the Potomac River; (b) the Corps could operate and maintain the presently non-functional Snake Island fishway located in the center of Little Falls Dam; and (c) the Corps could design and construct a new fishway with funds provided by the mitigation agreement with the Port America development.

In Virginia, American shad originally migrated about 465 km up the James River to spawn.³ A series of five dams constructed in the Richmond area beginning in 1804 blocked adults from over 300 km of potential spawning habitat. Presently, three of the five dams (Manchester, Brown's Island, Belle Isle) are partially negotiable by adult American shad at most river levels. Fish passageways are planned for the two remaining dams: William's Island and Boshers. Scott's Mill Dam, the first dam in the series of seven around Lynchburg (224 km upstream from Richmond) recently was granted a license for hydropower generation by the Federal Energy Regulatory Commission.¹⁷ The license contains requirements for fish passage, if and when fish reach the dam and fishery agencies deem fish passage is needed. The first two of four dams on the Appomattox River near Petersburg also were recently issued hydropower licenses that contain provisions for fish passage. The Appomattox River is a major tributary that joins the James River downstream from Richmond.

On the Chickahominy River, another major tributary of the James River below Richmond, a low head dam was built about 30 km upstream from the confluence in 1943. The area below this structure (Walker's Dam) was once the downstream limit of American shad spawning in the Chickahominy River, but now it is the only spawning area. At present, there is no fishery for American shad in the Chickahominy River.³ The city of Newport News supported the construction of two Denil-type fishways at Walker's Dam in 1988. River herrings were documented using the fish passage facilities in spring 1989.¹⁵ No use of the passage fish facilities by American shad has yet been observed.

The Embrey Dam at Fredericksburg blocks about 110 km of the mainstem Rappahannock River to American shad spawning runs, and is the only obstruction to anadromous fish migration on this river. The dam, located just above the fall line, recently was licensed for hydropower generation.¹⁷ The license includes requirements for fish passage.

Dams and impoundments also are viewed as factors that have contributed and are probably still contributing to the decline of American shad populations in North Carolina,

South Carolina, Georgia and Florida.¹²⁴ Major restoration efforts focused on reopening historical spawning sites blocked by dams are also presently underway in Maine, New Hampshire, Massachusetts and Rhode Island.¹²² A major program has been underway since the mid-1950's on the Connecticut River. The successes of these restoration programs have generally been encouraging but not yet conclusive.

Large tidal hydroelectric projects are being considered for construction in two or more basins of the Bay of Fundy, Canada.³⁴ These proposed projects, if implemented, pose a major threat to American shad populations from Chesapeake Bay and other east coast rivers. Extensive tagging studies carried out by Dadswell and his co-workers revealed that American shad from all east coast stocks migrate northward and use the basins in the Bay of Fundy as feeding areas during the summer.^{34,35} Construction of these large tidal projects would pose a threat to the migrating fish from turbine mortality, since the fish would be exposed to turbine passage with each tidal cycle. Neither of the proposed tidal projects currently is being developed, but if demands for electrical power increase, supplies of fossil fuels decrease, or prices for fossil fuels increase, development of this new hydropower technology could proceed rapidly.¹²²

Erosion

We could find no information which would directly implicate erosion as a factor which contributed to the Bay-wide decline of American shad populations. Severe floods, intensive agriculture, urban development, stream channelization, and roadway construction in the watersheds of Chesapeake Bay tributaries can accelerate the erosion of surface soils during stormwater runoff and increase levels of suspended solids and siltation rates in water courses. Periodic floods are normal occurrences in American shad spawning and nursery areas that should not affect stock abundance over the long run.

However, the turbid water and high flows associated with the severe flooding caused by Tropical Storm Agnes in June 1972 may have contributed to the failure of the 1972 year class in Virginia rivers.^{2,85} In Maryland, the Bay-wide juvenile abundance index for American shad was about average in 1972, but the 1973 and 1974 indices were very low.¹³⁵ In 1972, the Potomac River index was relatively high, but the upper Bay index was very low.¹²²¹ The effects of tropical storm Agnes on American shad reproduction in Maryland appeared to vary among river systems, but apparently was less severe overall than in Virginia. Refer to the section on **Suspended Solids** for sensitivities of American shad early life stages to erosion-related changes in habitat quality.

Fishing Pressure

Overharvesting has been suggested as one of the major factors involved in the dramatic decline in American shad stocks along the Atlantic seaboard between the late 1800's and the 1940's, and also may be a current deterrent to their recovery.^{99,148} The specific role of fishing pressure on American shad stocks in Maryland and Virginia since the 1950's is unclear. As stocks declined in Virginia, so did fishing effort, because many fishermen switched to larger mesh gear and pursued the equally scarce but more valuable striped bass.² Information is spotty about trends in fishing effort directed at the commercial or recreational fisheries for American shad in Maryland prior to the closure of the fishery in 1980.⁷³ In 1975, 344 people were involved in the commercial harvest; but by 1980, this number decreased to 115.

Landings of American shad in the ocean fishery (termed coastal intercept fisheries) along the eastern seaboard of the U.S. increased more than five-fold between 1978 and 1988.⁵² All Atlantic coast states have intercept fisheries for American shad, either directed or by-catch, that are conducted primarily with gill nets during late winter and early spring. These intercept fisheries harvest adults of various spawning river origins and capture fish that are en route from overwintering to spawning areas. Ocean harvest of American shad is dominated by four states: New Jersey, South Carolina, Virginia and Florida. In Maryland and Virginia, the ocean shad fisheries are directed rather than by-catch, usually begin in early February, and continue through early to late April.

About 20% of the fishing effort in Maryland occurs within about three miles of shore, in Assawoman and Chincoteague Bays and in National Marine Fisheries Service (NMFS) Sectors 621 and 622.⁵² All fish are landed at Ocean City. Between 1978 and 1990, the reported annual landings of American shad in Maryland's ocean fishery ranged from only 15 kg in 1981 to 222 x 10³ kg in 1989 (personal communication: H. Speir, MDNR). About 93% of the harvest occurred during March and April.

In Virginia, the ocean fishery directed at American shad is distributed along the entire coast, with most of the catch harvested by gill nets, haul seines and bottom trawls within three miles of shore.⁵² Most of the fish are caught in NMFS Sectors 625, 631 and 621, and landed at several ports. Between 1978 and 1990, reported annual landings of American shad in Virginia's ocean fishery (including seaside bays) ranged from 6 x 10³ kg in 1978 to 293 x 10³ kg in 1984.

The recent Alosid Management Plan for Chesapeake Bay¹⁸ recommended that coastal tagging programs be implemented to determine which American shad stocks are exploited in the ocean fishery. Given the location of a major overwintering area for Atlantic coast stocks (off

North Carolina) and the distribution of fishing effort (north of the entrance to Chesapeake Bay), it is unlikely that Maryland's ocean fishery for American shad harvests any Chesapeake Bay stocks. Rather, the fishery probably intercepts mostly Delaware and other more northern stocks as the adults migrate from overwintering areas to their spawning rivers. The ocean fisheries in Virginia and North Carolina almost certainly exploit American shad stocks that spawn in Chesapeake Bay tributaries and more northern rivers.⁵²

Early studies of American shad population dynamics reported that the number of juveniles produced is directly related to the number of adults that spawned.^{144,147} More recent studies found deficiencies in some of the earlier work, and concluded that year class strength may be related to spawning stock abundance, but appears to be most heavily influenced by environmental variables.⁷⁸ Studies of American shad in the Connecticut River^{29,31} showed that stock size had almost no influence on the number of recruits that returned to spawn. The determining factors that appeared to control year class in this population were environmental and focused on the pre-juvenile stages.

These findings for the Connecticut River, where American shad landings have remained relatively stable over the past 20 years,¹²² may not be completely relevant to Chesapeake Bay where American shad stocks declined to very low levels in the mid-1970's. Fisheries researchers acknowledge that at relatively low spawner population levels, near the critical threshold, total run size and fecundity should play a greater role in determining the number of young produced than when the stock is relatively abundant. What the critical stock size thresholds are for American shad spawning stocks in Maryland and Virginia is not known. Therefore, the decision to prohibit commercial and recreational harvests of American shad in Maryland waters of Chesapeake Bay in 1980 was wise, given the currently low stock abundance in all Maryland rivers.

HICKORY SHAD Contaminants

We could find no information on the effects of contaminants on any life stage of hickory shad.

Nutrients

We could find no information which would implicate high nutrient levels as a factor which directly contributed to the decline of hickory shad populations in Chesapeake Bay. Rulifson *et al.*¹²⁴ mentioned low DO, sewage outfalls, poor water quality, and non-point source pollutants as nutrient-related factors that were "possibly important or very important in contributing to the decline of certain populations of hickory shad" in North Carolina, South Carolina, Georgia, and Florida. Nutrient reduction is a

major goal of the 1985 Chesapeake Bay Restoration and Protection Plan.^{33,136}

Parasites and Diseases

We could find no information which would implicate parasites and diseases as factors which have contributed to the decline of hickory shad populations in Chesapeake Bay. Hickory shad can be afflicted with several parasites including nematodes (*Ascaris* spp.), larval cestodes, *Scolex polymorphus*, and trematodes.⁸² Digenetic trematodes were identified in the stomachs of adult hickory shad collected in the St. Johns River, Florida.¹⁵⁴

Impediments to Spawning Migrations

Man-made dams, impoundments, stream flow gauging weirs, roadway culverts, bridge aprons, and other impediments to upstream spawning migrations such as waterfalls, beaver dams, and log-debris piles have been implicated in Chesapeake Bay as factors which may be contributing to the delay in recovery of hickory shad populations. Other factors must have been involved in the drastic declines which occurred Bay-wide in the 1970's, because most major blockages were in place before the major stock declines began and some river systems do not have dams or other impediments to spawning migrations, yet these stocks have also declined.

Maryland DNR and the Chesapeake Bay Program are concerned that stream blockage is a factor which may be contributing to the delayed recovery of hickory shad and other alosid stocks.¹⁷ In Virginia and several southeastern states, the construction of impoundments on coastal rivers also has resulted in a loss of spawning habitat and is viewed as a factor which likely contributed to the decline of hickory shad populations.^{3,124}

Erosion

We could find no clear linkage between erosion and the Baywide declines in hickory shad stocks. Periodic floods are normal occurrences in hickory shad spawning and nursery areas that should not adversely affect stock abundance over the long run. However, the turbid water and high flows associated with the severe flooding caused by tropical storm Agnes in June 1972 probably contributed to the decimation of the 1972 year class of hickory shad in Maryland¹²⁶ and in Virginia,² significantly altered important spawning areas, may have contributed to reduced reproductive success for several years, and added another environmental stressor on an already stressed population.

Between June 21 and 23, 1972, the entire Bay watershed was subjected to measured rainfall in excess of 127 mm, with about a third of the region receiving more than 305 mm. Isolated locations recorded 457 mm during the three-day period.¹⁹ Most rivers crested at levels higher than previously recorded. Hickory shad larvae and juveniles may have been destroyed through physical damage from

high concentrations of suspended solids, by displacement downstream to areas of low food availability, and from osmotic stresses. Erosion stimulated by normal and intense rainfall events, flashy stormwater runoff episodes, and subsequent siltation in spawning areas, exacerbated by careless land use practices represents a habitat quality problem that is likely to be detrimental to hickory shad reproduction in many Bay tributaries.

Fishing Pressure

We could find no information which would implicate fishing pressure in Chesapeake Bay and its tributaries as a factor which contributed to the decline of hickory shad populations. Estimates of fishing mortality rates for hickory shad in the Bay do not exist.⁷³ Information on effort trends in the commercial or recreational fisheries prior to the 1980 Maryland closure is limited. Numbers of watermen who reported that they caught at least one pound of hickory shad declined from 150 in 1975 to 47 in 1980.⁷³ The recreational fishery for hickory shad in Maryland was concentrated in two tributaries of the lower Susquehanna River, Octoraro and Deer Creeks. We could find no information on the number of anglers that fished for hickory shad in these streams.

Some investigators have suggested that the offshore foreign fishery had a detrimental effect on all east coast alosid populations, including hickory shad, in the late 1960's and early 1970's.^{56,57} Unfortunately, there are no data to support the view that this offshore fishery caught substantial numbers of hickory shad. The offshore foreign fishing fleets, primarily from the USSR, East Germany, Bulgaria, and Poland, began operating off the Delaware, Virginia and North Carolina coasts in 1967. This fishery harvested immature river herrings and other alosids that eventually would have matured and spawned in rivers of the mid-Atlantic states. Since 1977, alosid catches by offshore foreign fishing fleets have decreased to relatively low levels as a result of agreements between the U.S. and foreign countries and enactment of the 200-mile Fishery Conservation Zone.²

SUMMARY AND RECOMMENDATIONS

AMERICAN SHAD

The American shad is the largest anadromous clupeid in the United States. Native to the Atlantic seaboard of North America, they are distributed from southeastern Labrador to the St. Johns River, Florida. Along the east coast of the U.S., American shad are most abundant from Connecticut to North Carolina. In the mid-Atlantic region, American shad historically spawned in New Jersey, Delaware and virtually all major tributaries to the Chesapeake Bay.

American shad live at sea and only enter fresh water in mid-February to early March to spawn. Peak egg deposition in the upstream reaches of Chesapeake Bay rivers

occurs during April. The juveniles move gradually downstream during the summer. Their seaward migrations accelerate from late October through late November when water temperatures fall below 15°C. The subadults and adults participate in extensive oceanic migrations from the Chesapeake Bay to summer feeding grounds as far north as the Bay of Fundy, Canada. Males and females reach sexual maturity at 4 and 5 years of age, and then return to their natal rivers to spawn. Repeat spawning ranges from about 20-37% in Chesapeake Bay populations.

Historically, American shad represented a major fishery resource all along the Atlantic seaboard. But between 1897 and 1940, annual harvests declined dramatically due to pollution and siltation of spawning rivers, overharvesting, and construction of dams which prevented access to spawning sites. Commercial landings of American shad in the Chesapeake Bay reached record lows in the late 1970's. In 1980, the commercial and recreational fisheries were closed in Maryland waters of Chesapeake Bay. American shad population levels in Virginia have been relatively low but stable since the late 1970's; therefore, fishing is still allowed.

Uncertainty surrounds any attempts to define the major factors responsible for the decline in American shad stocks throughout Chesapeake Bay. Gradual loss of spawning habitat quantity and quality and overharvesting during the 1800's and through the first half of the 1900's are the major explanations offered for the large population declines during this period. Fishing pressure has eased substantially since the mid-1950's. But until the 1980's, efforts to restore lost spawning habitat were limited and generally unsuccessful. Both Maryland and Virginia currently are engaged in restoration efforts designed to supplement natural reproduction with hatchery-reared young (Susquehanna River) and provide fish passage facilities at existing dams (in several rivers) to reopen lost spawning habitats. Current restoration programs focused on fish passage and designed to increase habitat quantity are encouraging, but their long-term achievements will take many years to be seen. These restoration efforts should continue and include sufficient intensive monitoring studies to evaluate their effects.

Other factors which also may be contributing to the depressed condition of the Bay stocks are receiving little attention. Concerns about the quality of American shad spawning and nursery habitats are clearly justified, but few studies are being directed at this topic. Acidic deposition and discharge of chlorinated sewage effluents are two of potentially many pollutant sources that may be slowing the recovery of depressed American shad stocks in Chesapeake Bay. Research should be directed at these issues.

Temptations to reopen the fishery for American shad in the Maryland portion of the Bay should be resisted until

adequate stock recovery is documented. If stocks do not show clear signs of recovery or decline further in Virginia, management options that include a moratorium on fishing should be considered. Harvests of adults in the coastal intercept fishery should be closely monitored and evaluated.

This survey of the literature on American shad suggests that the critical life history stages are the egg, prolarva (yolk-sac or prefeeding larva), postlarva (feeding larva, and early juvenile (through the first month after transformation). The critical life history period is April through July. A matrix of habitat requirements for the critical life stages is presented in Table 1.

HICKORY SHAD

The hickory shad is a medium-sized anadromous clupeid that occurred historically along the east coast of North America from the Bay of Fundy, Canada, to the Tomoka River, Florida. This alosid species is now most abundant from New York southward, but hickory shad probably do not spawn north of Maryland. In Chesapeake Bay, hickory shad are near the northern limits of their spawning range and probably never have been abundant, although they were harvested throughout the Bay prior to the 1970's.

The hickory shad is somewhat of a mystery to both fishermen and ichthyologists because so little is known about its basic life history. In Chesapeake Bay, hickory shad spawning runs typically began during March and April, with spawning activity occurring between late April and early June. Specific spawning sites are not well documented, but they appear to be concentrated in mainstem reaches of rivers upstream from the major spawning sites for American shad. Juvenile hickory shad appear to migrate directly to saline areas during the summer and may not use oligohaline portions of Bay estuaries as nursery areas.

Records of commercial landings support the view that hickory shad populations throughout the Chesapeake

Bay declined dramatically during the early to mid-1970's. Loss of spawning habitat quantity and quality, heavy exploitation in the offshore foreign fishing between 1967 and 1977, and decimation of the 1972 year class and alteration of many spawning areas by tropical storm Agnes are major factors that probably were involved in the population declines, or are acting to slow any stock recovery. Commercial and recreational fishing for hickory shad was closed effective January 1981 in Maryland waters, but not in Virginia. Given the currently low stock abundance levels, a Baywide moratorium on fishing for hickory shad should be implemented and continued until the stocks show clear signs of recovery.

Hickory shad populations in Maryland are at such low levels of abundance that natural stock recovery may be very slow in coming, if it can occur at all. Carefully designed restocking efforts may be needed if adult hickory shad can be transported from areas where they are relatively abundant or the eggs and larvae can be reared in fish hatcheries. In Virginia, the prognosis for stock recovery is somewhat more optimistic. Current programs and plans for fish passage facilities in both states should increase the quantity of spawning habitat available to remnant hickory shad populations. However, until we understand more about hickory shad life history and population dynamics, it will be difficult to determine what specific resource management actions, in addition to the current closure of the fisheries in Maryland, should be taken to rebuild Baywide stocks.

The critical life history stages of hickory shad are the egg, prolarva, postlarva and early juvenile. The critical life history period is March through July. Available information was not adequate to construct a matrix of life history requirement for any life history stage.

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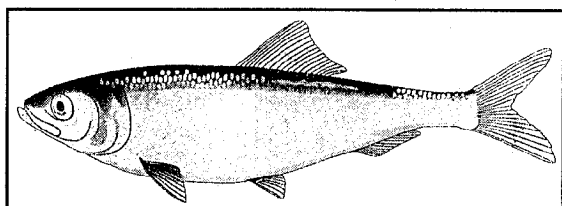
Table 1. Summary of habitat requirements for American Shad.

Life Stage	Temperature °C	Salinity ppt	pH	Dissolved Oxygen mgL ⁻¹	Suspended Solids mgL ⁻¹
Egg	13.0-26.0	0-15	> 6.0	> 5.0	< 1000
Larvae	15.5-26.1	NA	> 6.7	> 5.0	< 100
Juvenile	15.6-23.9	0-30	NA	> 5.0	< 100
Adult	10-30	0-30	NA	> 5.0	< 100

ALEWIFE AND BLUEBACK HERRING

Alosa pseudoharengus and *Alosa aestivalis*

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Alewife and blueback herring are relatively small anadromous fish of the family Clupeidae. Spawning habitats of these "river herring", include freshwater, non-tidal areas of smaller tributaries of Chesapeake Bay. River herring juveniles leave their nursery areas in fall, mature in the Atlantic Ocean, and return after two to five years to Bay tributaries for spring spawning.

River herring supported relatively important commercial fisheries in Chesapeake Bay until the early 1970's when stocks began to decline dramatically. Current landings are the lowest on record. Probable causes of stock declines include loss of spawning and nursery habitat quantity and quality, over-exploitation of primarily immature individuals in the offshore foreign fishery between 1967 and 1977, and decimation of the 1972 year classes and alteration of spawning habitats by tropical storm Agnes.

The critical life history stages of alewife (AW) and blueback herring (BH) are the eggs, larvae, and early juveniles. Water temperatures $> 11^{\circ}\text{C}$ (AW) and $> 14^{\circ}\text{C}$ (BH), $\text{pH} > 5.0$ (AW) and > 5.7 (BH) and dissolved oxygen (DO) $> 5.0 \text{ mgL}^{-1}$ are important habitat requirements for eggs. Larvae require water temperatures at least 8°C (AW) and 14°C (BH), $\text{pH} > 5.5$ (AW) and > 6.2 (BH), $\text{DO} > 5.0 \text{ mgL}^{-1}$, and suspended solids $< 500 \text{ mgL}^{-1}$. Major habitat concerns for river herring are stream acidification; stream blockages; and land use changes that alter stormwater runoff patterns, accelerate erosion, and increase sedimentation.

Chesapeake Bay stocks of river herring have continued to decline. Degradation of spawning and nursery habitats from acidic deposition and land use changes, and continuing (albeit reduced) foreign, joint-venture, and local fishing pressure, may constitute significant increments of mortality on immature and adult river herring that the populations currently are ill-equipped to bear. Mitigation of stream acidification, removal of spawning stream blockages, implementation of effective stormwater management practices, and Baywide harvest restrictions are positive steps that should be taken to encourage recovery of these depressed populations.

INTRODUCTION

The alewife is an anadromous clupeid that is smaller than the American shad and the hickory shad, but about the same size as the blueback herring. Maximum length is about 380 mm.⁶⁷ Alewife are grayish-green above and silvery on the sides and belly.¹⁵¹ Neves¹¹⁷ associated the

greenish coloration of the alewife with its deeper vertical distribution (56-110 m) relative to blueback herring (27-55 m) in coastal waters.

Adult alewife can be distinguished externally from adult blueback herring by their strongly compressed, deep, and less elongated body; terminal mouth with the lower jaw

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projecting slightly; and large eyes with the diameter greater than the snout length. Alewife have a pale to dusty-colored peritoneum. Chambers *et al.*¹⁶ described a technique for distinguishing larval alewife from larval blueback herring in the 5-16 mm standard length (SL) range. The technique relies primarily on differences in the number of myomeres (body segments) between the insertion of the dorsal fin and the posterior margin of the vent.

The blueback herring is an anadromous clupeid that is about the same size as the alewife. Maximum length is about 380 mm.⁶⁷ Blueback herring are bluish above with silvery sides. Adult blueback herring can be distinguished externally from adult alewife by their less compressed and more elongate body, and by their smaller eyes, with the diameter equal to or less than the snout length. Blueback herring have a sooty to black peritoneum. Blueback herring and alewife juveniles also can be separated by scale morphology with some magnification (personal communication: J. Loesch, Virginia Institute of Marine Science).

DISTRIBUTION

Alewife are distributed from at least Paquet, in north-eastern Newfoundland, to South Carolina.^{67,151} Reports of alewife in Florida waters are questionable.¹⁴⁵ Alewife are abundant in the mid-Atlantic and northeastern states. Alewife are the dominant (> 90%) river herring species throughout New England, but not in the Connecticut River, in the St. John River estuary of New Brunswick and in coastal ponds and streams of Atlantic Nova Scotia.⁸⁷ In the mid-Atlantic region, alewife occur in virtually all tributaries to Chesapeake Bay, in Delaware, and in New Jersey.⁶⁷ Alewife have become landlocked in many parts of eastern North America. Landlocked populations occur in the Great Lakes, several of the Finger Lakes in New York, and other freshwater lakes.^{67,142}

Blueback herring are distributed from Cape Breton, Nova Scotia¹⁵⁰ to northern Florida.^{50,184} Blueback herring are the dominant river herring species in the Gulf of St. Lawrence region where there are few lakes.⁸⁷ Blueback herring are most numerous in warmer waters from Chesapeake Bay south.^{96,151} In the mid-Atlantic region, blueback herring occur in Chesapeake Bay, in virtually all tributaries to Chesapeake Bay, in the Delaware River and in adjacent offshore waters.⁶⁷ Landlocked populations of blueback herring occur in some areas of the southeastern U.S. (e.g., Clayton Lake, Virginia).

LIFE HISTORY

ALEWIFE

Spawning Activity

Schools of adult alewife restrict their oceanic movements to coastal areas near natal estuaries and rarely are collected more than about 130 km from shore.⁶⁷ The onset

of spring spawning is related to temperature and thus varies with latitude. At the extreme southern end of their range (North Carolina), alewife begin spawning in late February, but they may not commence spawning until late April or early June at the northern end of their range.⁸⁷ Males tend to precede the females onto the spawning areas.¹³⁸

Alewife may return to natal streams for spawning. This conclusion is supported by morphometric and meristic (segmental) differences among fish from different systems,¹⁰⁷ establishment or reestablishment of spawning runs by stocking gravid adults,⁴⁷ olfaction experiments,¹⁷⁰ invasions into new systems (e.g., Great Lakes) and rapid abundance increases within systems where fish passage facilities were constructed (e.g., above the Holyoke Dam on the Connecticut River).

In Chesapeake Bay, the onset of alewife spawning migrations is typically from early to mid-March through April, when water temperatures range from 10-18°C.^{67,87,114} Temperatures below 8°C and above 18°C (24 h average) result in little adult movement into spawning streams.¹³⁷ Egg deposition commonly occurs at water temperatures between 10-22°C, but ceases above 27-28°C.⁶⁷ In the Patuxent River, Maryland, alewife spawning was observed at temperatures from 11-19°C.¹¹⁴

Upstream movements onto the spawning grounds are influenced by light intensity (most movement during daylight hours), water flow (more movement during higher flows) and temperature.^{24,137} Alewife adults generally do not jump over obstructions on the spawning run, but they easily can negotiate riffles and fishways¹⁵¹ with little apparent physiological stress.³² Cooper²⁵ observed that adult alewife lost body weight (on average, 50 g for females and 36 g for males) during the spawning migration to Pausacaco Pond, Connecticut. He attributed these weight losses to the physiological demands of the spawning migration, absence of feeding for an extended time, the warm environment of the pond, and spawning activity.

Several groups or "waves" of adult alewife arrive at the spawning sites, deposit their eggs during a period of two to three days and then move quickly downstream.^{25,72,73} Spawning activity occurs day and night, but is apparently greater at night.⁴³ Several investigators have observed that the larger and older alewife spawn first; the smaller and younger fish spawn progressively later.^{25,73,83,84}

Alewife tend to favor slow-moving sections of streams or coastal ponds and lakes for spawning sites.⁸⁷ However, they are reported to spawn in a variety of habitats with substrates ranging from coarse gravel to organic detritus.⁶⁷ Spawning alewife and blueback herring are isolated spa-

tially, to a large degree, within their sympatric range,⁸⁷ but some overlap can occur.⁶

During the spawning act, single female alewife swim close to shore accompanied by many males.²⁵ Groups of spawning fish swim in circular patterns just below the surface. Eggs and sperm are extruded simultaneously and broadcast at random into the water column and over the substrate. Spent adults migrate rapidly downstream after spawning.

Egg and Larval Development

The fertilized eggs are semi-demersal to pelagic, slightly adhesive until they become water-hardened and average about 1.1-1.2 mm in diameter.^{25,67} Alewife eggs are slightly larger than blueback herring eggs, but do not contain oil globules.¹⁷⁵ Incubation periods for alewife eggs are 2.1 days at about 29°C, 3.7 days at about 21°C,³⁹ 3.4-5 days at 10.0-12.2°C,²⁰ 6 days at 15.6°C⁴⁸ and 15 days at about 7°C.³⁹

The relationship between temperature and incubation time can be described by this equation:³⁸

$$t = 6.335 \times 10^6 (T)^{-3.1222}$$

where t = time in days and T = temperature in °F. Average time to median egg hatch ranges from 7.4 days at 12.7°C to 3 days at 23.8-26.8°C.⁷¹ The optimum temperature for alewife eggs is 17-21°C. No eggs hatched at 29.7°C. Alewife eggs can tolerate water temperatures between about 7-30°C, but a high proportion (69%) of deformed larvae were produced from eggs incubated below about 11°C.^{38,71}

Yolk-sac larvae range from about 2-5 mm total length (TL) at hatching and begin exogenous feeding at three to five days posthatch.^{22,67} Within about ten days, the larvae are 6 mm long.⁸¹ Survival of unfed alewife larvae increased from 3.8 days at about 11°C to 7.6 days at about 15°C and then decreased to 2.4 days at 17-18°C.³⁸ Even though alewife eggs hatch and the larvae live for a time at temperatures as low as 7°C, development of a functional jaw does not occur at temperatures below 10°C.³⁸

The yolk-sac larvae are positively phototropic⁹⁷ and exhibit alternate active vertical movements toward the surface and passive vertical descents.²² The larvae form schools within two weeks after hatching.²⁵ At seven constant temperatures between 12.9 and 29.1°C, average daily rates of larval weight gain during the first 12 days post-hatch increased directly with temperature to a maximum of 83.8 $\mu\text{g d}^{-1}$ (dry weight) at the highest rearing temperature (29.1°C). The maximum net biomass developed at 26.4°C. Feeding alewife larvae transform gradually to the juvenile stage at about 20 mm TL, and usually are fully scaled at 45 mm TL.¹²⁰

Juveniles

Juvenile alewife tend to remain in the tidal freshwater nursery areas in spring and early summer, but they also may move upstream in summer with the encroachment of saline water.¹⁷⁶ As water temperatures decline in the fall, the juveniles move downstream during the first phase of their seaward migration.⁸⁷ These seaward movements apparently are stimulated by abrupt water temperature declines, increases in flow and precipitation, but not size or age.^{25,73,138,139} Juvenile alewife tend to emigrate from the freshwater nursery areas to more brackish areas about a month earlier than juvenile blueback herring.^{73,86,146} Some juvenile alewife remain in deep estuarine waters through the winter.⁵¹

During their fall seaward emigration through the nursery areas, juvenile alewife tend to concentrate near the bottom during the day and migrate upward toward the surface at night.⁸⁷ However, a partial spatial segregation of juvenile alewife and juvenile blueback herring was observed in bottom trawl and surface trawl catches.⁹² Juvenile alewife tended to be deeper in the water column than juvenile blueback herring, especially at night. Vertical separation of these two alosid species could reduce interspecific competition for food.⁸⁷

Young alewife apparently grow faster than young blueback herring, at least in Chesapeake Bay.⁵¹ A portion of this difference likely is due to the earlier spawning period for alewife and the longer growing season.⁴⁰ Growth rates ranging from 4-20 mg d^{-1} were documented for juvenile alewife in the James River, Virginia.¹⁷⁷ Growth of young alewife between hatching and fall emigration from the nursery areas averaged 102 mm TL in the lower Chesapeake Bay⁶⁹ and 113 mm TL in the Connecticut River.⁹⁸ In the Neuse River, North Carolina, juvenile alewife increased in length from 35 mm in June to 75 mm in August.⁴⁸ Richkus and DiNardo¹⁴⁰ reported daily growth rates for juvenile alewife of 0.625 mm (New Jersey) and 0.820-0.996 mm (Massachusetts).

Data on mortality rates of juvenile alewife are meager. Richkus¹³⁷ reported a 75% mortality rate for juveniles over a six week period prior to their emigration from a pond in Rhode Island.

Subadults and Adults

Little information is available on the life history of subadult and adult alewife after they emigrate to the sea as young-of-year or yearlings, and before they mature and return to fresh water to spawn. Like other anadromous clupeids, alewife may exhibit seasonal movements in conjunction with preferred isotherms, but direct evidence is lacking.⁴⁰ Juvenile alewife 70-100 mm fork length (FL) were most numerous between December and April 1972-1975 in ocean waters out to at least 8 km from the southern New Jersey coast.¹⁰⁸ Juveniles were collected during the

daytime in bottom trawls operating at 2.4-19.2 m depths, where bottom salinities and temperatures ranged from 23.0-32.0 ppt and 2.0-10.0°C. This area appears to be an important overwintering ground for juvenile alewife originating from the Hudson and Delaware rivers and numerous smaller spawning streams along the New Jersey coast. Another overwintering area for young alewife is located off the North Carolina coast.⁵⁴ In 1978, most young alewife were collected during February at depths ranging from 19-36 m from 18 km NNE of the Cape Hatteras Lighthouse to the mouth of Chesapeake Bay.⁶⁴

Sixteen years of trawl survey data collected along the Atlantic coast between Cape Hatteras, North Carolina, and Nova Scotia, Canada were summarized by Neves (1981).¹¹⁷ Alewife ranging in size from 60-350 mm FL were taken in greatest numbers at depths between 56-110 m and outnumbered blueback herring by about 10:1. During summer and fall, catches of alewife were confined to the sampling area north of 40° north latitude; spring catches were distributed over the entire Continental Shelf in the study region.

Alewife spawning stocks contain primarily ages III-VIII individuals, with the modal group generally ages IV or V.⁸⁷ Males tend to dominate age groups III-V; females live longer and dominate the older age groups. From a synthesis of available data, it was reported that 82-100% of male alewife and 60-95% of female alewife mature by age IV.^{133,134} In North Carolina stocks, some males can mature and spawn at age II.¹⁴⁰

Recent surveys by the Maryland Department of Natural Resources (MDNR) in Maryland rivers indicate that alewife spawning runs are dominated by ages IV-VI fish.^{55,81,123,178,179} Ages IV and V fish are mostly males; ages V, VI, and VII fish are predominantly females. Recent surveys by the Virginia Institute of Marine Science (VIMS) in Virginia rivers indicate that the modal groups for alewife spawning runs in the Rappahannock and York Rivers are ages IV-V and V-VI, respectively.^{8,93} Female length at age is consistently greater than male length at age in Maryland rivers^{55,81} and in other coastal stocks.¹⁴⁰ Age IV males collected during spring 1989 in the Nanticoke River, Maryland, averaged 236 mm FL and 188 g wet weight.⁵⁵ Age IV females averaged 244 mm FL and 223 g. Alewife from northern stocks tend to be larger at age than alewife from southern stocks.

The percentage of repeat spawners and longevity in alewife populations seems to decrease from north to south,⁴⁰ however, Richkus and DiNardo¹⁴⁰ disagreed with this observation. Krauthamer and Richkus⁸¹ stated the broad generalization that repeat spawners typically comprise 30-40% of alewife spawning runs. The percentage of repeat spawners was 60% in Nova Scotia,¹²⁸ 30-72% in Maryland,^{55,178} 61% in the York River, Virginia,⁶⁹ and

< 10% in North Carolina.¹⁷² The substantial percentage of repeat spawning in alewife populations from the Chesapeake Bay is relevant to management strategies.⁸¹ Heavy exploitation of spawning runs can preclude the potential for repeat spawning. If repeat spawning is needed for Bay stocks of alewife to persist in the face of fishing pressure and habitat deterioration, loss of repeat spawning capacity could be a serious threat to stock viability. No alewife older than age IX have been captured in North Carolina,^{63,167} but age X alewife were recorded in New Brunswick⁶² and Nova Scotia.¹²⁸

Fecundity of alewife is related to age, stock origin and size, and is highly variable. Estimates of fecundity for anadromous alewife populations range from about 100,000-467,000 eggs per female.¹³⁴ Female alewife collected in the Potomac River during the early 1900's contained an average of 102,800 eggs.¹⁵⁵ Alewife fecundity in the Patuxent River ranged from 168,000-170,829 eggs per female in the 1980's.¹¹⁵ Although different methods of estimating fecundity can introduce unknown biases into the data and make direct comparisons across studies difficult, the alewife clearly is a high fecundity species.^{87,140} Maximal alewife fecundity occurs between ages V-VII, and then declines for older females.^{57,102}

Sex ratios (male:female) in alewife populations throughout a single spawning season or over several years tend toward 1:1, or sometimes favor males.⁸⁷ Sex ratios for alewife in the Patuxent River (1981) and in Fishing Bay (1982), Maryland, were 1.01:1 and 1.50:1.⁸¹ O'Dell and Mowrer¹²³ reported a male: female sex ratio of 1:1.29 in the Upper Bay area, a statistically significant departure from a 1:1 ratio. Sex ratio estimates can be influenced by several factors.⁸⁷ For example, males tend to dominate the early portion of the spawning season, but the proportion of females typically increases toward the end.^{25,73} Female alewife in the process of spawning generally attract several males,¹³⁴ and as many as 25 male alewife may attempt to spawn with a single female.⁴

BLUEBACK HERRING Spawning Activity

Schools of adult blueback herring inhabit a narrow band of coastal waters and move to predominantly fresh or slightly brackish areas in the spring to spawn.⁶⁷ The onset of spawning is related to temperature and thus varies with latitude.⁸⁷ At the extreme southern end of their range (Florida), spawning can begin in December or January, but may not commence until June near the northern end of their range (New Brunswick) and can continue through August.⁹⁹ Males usually arrive at the mouths of spawning rivers earlier than females, but the proportion of females increases as the spawning season progresses.⁸⁷

In Chesapeake Bay, the primary spawning runs of blueback herring begin in early April in lower Bay tributaries

and in late April in the upper Bay, about three to four weeks after the peak alewife runs.⁵¹ Blueback herring may return to natal rivers for spawning. However, spawning stocks also can stray to adjacent streams.¹⁰⁷ The spawning period extends from about mid-April through late May in Chesapeake Bay tributaries, when water temperatures typically range from 14-25°C.⁶⁷ Mowrer¹¹⁴ observed blueback herring spawning activity in the Patuxent River, Maryland, at temperatures of 15-22°C. Optimal spawning temperatures are between 21-25°C.

Blueback herring spawn in freshwater and slightly brackish habitats, sometimes near tidewater, in small tributaries and often migrate far upstream to spawn.⁶⁷ Upstream distribution of gravid adults is a function of habitat suitability and hydrologic conditions permitting access to these sites.⁹⁵ In coastal New England rivers where blueback herring are sympatric with alewife, adult blueback herring prefer to spawn where flows are relatively swift and over gravel and clean sand substrates; they seem to avoid lentic areas.^{86,87} In southeastern U.S. waters, where alewife are few, blueback herring exhibit more variety in their selection of spawning grounds and deposit eggs over shallow areas covered with vegetation, in ricefields, in swampy areas and in small tributaries upstream from the tidal zone.^{21,87,104,145}

Loesch⁸⁷ suggested that the preference of blueback herring for lotic spawning sites in the north and lotic and lentic sites in the south is a clinal spawning pattern that may reduce competition with alewife for spawning grounds when the two alosid species are sympatric. Unfortunately, the spawning behavior of blueback herring and alewife near the middle portion of their ranges (e.g., Chesapeake Bay) has not been studied to confirm Loesch's clinal hypothesis.

Groups of adult blueback herring engaged in spawning behavior are usually composed of a single female encircled by several males swirling together as the eggs and sperm are broadcast simultaneously over the substrate, where the fertilized eggs adhere to rocks, gravel and debris.⁹⁵ Total spawning time for a single migratory group or "wave" of spawners is typically five days or less.⁹⁵ Spawning migrations are influenced by several physical and chemical factors, with temperature playing a major role.²⁴ Spent adults migrate rapidly downstream after spawning.

Egg and Larval Development

The fertilized eggs are essentially pelagic, demersal in still water, somewhat adhesive until water hardened, average about 0.9 to 1.1 mm in diameter,^{67,99} and are slightly smaller than alewife eggs.¹⁷⁵ Incubation times for blueback herring eggs range from 94-80 h at 20-21°C and from 58-55 h at 22.2-23.7°C.^{22,109,165}

Yolk-sac larvae are 3-5 mm TL at hatching.⁶⁷ They average about 5 mm TL when they absorb the yolk, and begin to feed exogenously at three to four days post-hatch. Blueback herring and alewife cannot easily be distinguished from each other as eggs or as larvae through about 15 mm long. A technique for distinguishing larval blueback herring from larval alewife in the 5-16 mm SL range was described by Chambers *et al.*¹⁶ The technique is time-consuming and relies primarily on differences in the number of myomeres between the insertion of the dorsal fin and the posterior margin of the vent. At body lengths greater than about 15 mm, the two river herring species generally can be separated on the basis of peritoneum color and eye size,⁹⁹ or scale morphology. Larval transformation to the juvenile stage is usually completed at about 20 mm TL. When the juveniles reach about 30 mm, they are morphologically similar to the adults.¹¹⁵

Juveniles

Juvenile blueback herring may move upstream in the nursery areas during summer periods of decreased flows and encroachment of saline water.¹⁷⁶ However, as water temperatures decline in the fall, the juveniles move downstream to more saline waters and begin the first phase of their seaward migration.⁸⁷ Juvenile blueback herring tend to remain in the natal rivers about a month longer than juvenile alewife before returning to the sea.^{72,86,146}

During a three year study of fall downstream migrations in the Connecticut River, juvenile blueback herring began to emigrate in September as water temperatures declined to 21°C.¹²⁷ Seaward migration peaked at 14-15°C and ended in late October or early November at 10°C. The juveniles actively moved throughout a 24 h period, with peak activity at 1800 hours. Some juvenile blueback herring overwinter in deep estuarine waters.⁵¹

During their fall seaward emigration through the nursery areas, juvenile blueback herring tend to concentrate near the surface at night and near the bottom during daytime.⁹² This general vertical diel migratory pattern also was exhibited by juvenile alewife; however, a partial spatial separation of juvenile alewife and juvenile blueback herring also was observed. Juvenile blueback herring were oriented more strongly to the surface at night than were juvenile alewife. These observed diel differences in vertical distribution of the juveniles may serve as a mechanism that could reduce interspecific competition for food between these two alosids.⁸⁷

Young blueback herring apparently grow slower than young alewife, at least in Chesapeake Bay.⁵¹ A portion of this difference is likely due to the later spawning period of blueback herring and the shorter growing season.⁴⁰ Krauthamer and Richkus⁸¹ summarized juvenile blueback herring growth rates that ranged from 0.208 mm d⁻¹ (Geor-

gia) to 0.209 mm d⁻¹ (Virginia) to 0.657 mm d⁻¹ (Connecticut). In the Cape Fear River, North Carolina, juvenile blueback herring averaged 49.3 mm FL in July and 57.4 FL in November (1964).³⁰ We could not locate any mortality rate estimates for juvenile blueback herring.

Subadults and Adults

Little information is available on the life history of subadult and adult blueback herring after they emigrate to the sea as young-of-year or yearlings, and before they mature and return to freshwater to spawn. Like other anadromous clupeids, blueback herring may exhibit seasonal movements in conjunction with preferred isotherms, but direct evidence is lacking.⁴⁰ New Jersey inshore waters out to at least 8 km from shore appear to provide an important overwintering area for young blueback herring less than about 120 mm FL that originate from spawning rivers in this region.¹⁰⁸ Neves¹¹⁷ summarized 16 years of trawl survey data collected along the Atlantic coast between Cape Hatteras, North Carolina, and Nova Scotia. Alewife outnumbered blueback herring about 10:1 in all samples combined. Most blueback herring were 60-350 mm FL and were taken in greatest numbers at depths between 27-55 m. During summer and fall, blueback herring apparently were confined to areas north of 40° and 43° north latitude; spring catches were distributed over the entire Continental Shelf in the study region.

Blueback herring reach sexual maturity at ages III-VI, but the composition of virgin female spawners is dominated by age IV fish.^{87,140,145} In 1982, the modal ages of blueback herring in Fishing Bay, Maryland, were IV for males and V for females.⁸¹ In the Patuxent River, Maryland (1981), male and female blueback herring were most numerous at age V.

Female length at age is consistently greater than male length at age in Chesapeake Bay populations of blueback herring and in other coastal stocks.¹⁴⁰ Age IV males collected during spring 1989 in the Nanticoke River, Maryland, averaged 227 mm FL and 153 g; age IV females averaged 236 mm FL and 176 g.⁵⁵ Differences in age at maturity among river systems are evident, but no distinct lateral gradient appears in the available data.¹⁴⁰

In general, repeat spawners comprise 30-40% of blueback herring spawning runs;¹⁴⁰ but there are reports of 65% repeat spawners in the York River, Virginia⁶⁹ and 75% repeat spawners in Nova Scotian waters.¹²⁸ Analysis of the spawning history of blueback herring from the lower Susquehanna River, Maryland, between the Conowingo Dam and Harve de Grace, showed that repeat spawning was 30%.¹³¹ In the Fishing Bay area of Maryland, about 45% of the blueback herring had spawned once, 21% had spawned twice, 7% three times and 1% four times.⁸¹

Fecundity of blueback herring is related to age and size, but is highly variable. Fecundity estimates for anadromous stocks range from about 33,000-400,000 eggs per female.¹³³ Mowrer¹¹⁵ estimated the fecundity of blueback herring from the Patuxent River, Maryland, at 121,342-228,922 eggs per female. The age-fecundity relationship may be asymptotic for blueback herring. Maximum fecundity occurs at about age VI, and "fecundal senility" appears to develop in chronologically or physiologically older fish.^{87,95}

Sex ratios (male:female) in blueback herring populations integrated over a season or combined across several years either tend toward 1:1 or sometimes favors males.⁸⁷ Sex ratios for blueback herring adults in the Patuxent River, Fishing Bay, and the upper Bay areas of Maryland were 1:08:1, 1.54:1, and 2:1 respectively.⁸¹ Male domination of the sex ratio is related to the greater proportion of males that mature at ages III and IV. Sex ratio estimates in blueback herring populations can also be influenced by spatio-temporal differences in behavior for males and females. Males are typically more numerous early in the spawning season, but the proportion of females increases toward the end.^{25,95} Males also tend to remain longer on the spawning grounds, and some may return in succeeding spawner waves.⁸⁶ Females attract several males during spawning behavior.

ECOLOGICAL ROLE

ALEWIFE

Food Habits

Alewife larvae are planktivores at about 6 mm long when they begin to feed on relatively small cladocerans (mainly *Cyclops* and *Limnocalanus*) and copepods, adding larger species to their diet as they grow.^{119,120} The larvae appear to be highly selective feeders.¹²⁰ Juvenile alewife in Hamilton Reservoir, Rhode Island, consumed primarily dipteran midges in July, but switched to cladocerans in August and September.¹⁷³ In the Cape Fear River, North Carolina, alewife juveniles consumed more ostracods, insect eggs and insect parts than did juvenile blueback herring.³⁰

Food habits of adult alewife are poorly documented. Stomachs from adults collected at sea contained mostly calanoid copepods, mysids, and other zooplankton.¹¹⁷ Stomachs of alewife collected from the offshore waters of North Carolina contained unidentified fish remains and various zooplankton such as amphipods, copepods, isopods, mysids, sagitta and decapod larvae.⁵⁴ Adult alewife prefer larger food organisms (such as amphipods and mysids) than adult blueback herring.¹⁶² Adult alewife do not feed extensively or often not at all during their upstream spawning migrations.^{5,23} After spawning, adult alewife feed on cases of the caddis-fly *Brachycentrus* in freshwater areas before emigrating seaward.²³

Competition and Predation

Alewife juveniles often coexist with blueback herring and American shad juveniles in the nursery areas during summer and fall. Hence, opportunity for interspecific competition is present.

Differences in juvenile diel activity patterns among the anadromous alosid species is one potential mechanism for reducing interspecific competition.^{87,92,146} Juvenile alewife and blueback herring may coexist in the Connecticut River by consuming different prey or selecting different sizes of prey.²⁷ Because alewife spawn earlier than blueback herring, juvenile alewife gain a size advantage that may reduce interspecific competition as they became more omnivorous with increasing size.⁶¹ Juvenile alewife in the Minas Basin, Nova Scotia, favored larger and more benthic prey items than did juvenile blueback herring.^{162,163} These observed differences in prey selection suggest that juvenile alewife employ a particle-feeding strategy while blueback herring are predominantly filter-feeders.

Feeding chronologies for juvenile alewife and blueback herring also appear to differ, and may serve to further reduce potential interspecific competition. Weaver¹⁷⁷ observed diurnal feeding by juvenile alewife with bimodal activity: a major peak occurred about one to three hours before sunset and a minor peak occurred about two hours after sunrise. In another study, juvenile blueback herring began to feed actively at dawn, increased their feeding activity through the day to a maximum at dusk. Feeding declined from dusk to dawn.¹³

Concerns about introducing alewife into closed freshwater systems, particularly when predator stocks are low, include uncontrolled population growth, competition with other fish species for food and space, selective feeding on zooplankton, piscivory and growth of the alewife beyond an acceptable prey size for predators.⁸⁷ Few of these potential problems have been observed after the establishment of anadromous alewife runs. Rather, the presence of anadromous alewife can contribute positively to freshwater ecosystems.⁸⁷ Anadromous alewife were a nutrient source to a pond in Rhode Island rather than just a mechanism for nutrient regeneration. Alewife mortality could reduce sedimentation rates in lakes by providing the nitrogen and phosphorous needed to stimulate microbial breakdown of leaf litter.³⁵

In landlocked systems, where young and adults can emigrate to the sea, alewife populations can influence the species, numbers and size composition of zooplankton communities. Hutchinson⁵⁸ demonstrated that alewife predation was responsible for a change in the zooplankton community of Black Pond, a 10 ha glacial lake in the Adirondack Mountains. Alewife were first stocked in this small lake as forage for landlocked Atlantic salmon. He

observed that large zooplankton species were replaced over a period of eight years by mostly small forms and some large species such as *Cyclops vernalis* and *Holopedium gibberum*. He concluded that the alewife population eliminated, through selective predation, most large zooplankton species from Black Pond. He also suggested that the reduced growth of Atlantic salmon in Black Pond during the study period may have been the result of competition with alewife for zooplankton. Studies in the Great Lakes indicate that alewife also can compete with other fish species for zooplankton prey^{156,157,183} by cropping off the larger species.¹⁸⁰ Alewife have at least three behavioral modes of zooplankton feeding that include size-selective and non-size selective consumption.⁶⁰

Intraspecific competition for food may be more severe than interspecific competition for alewife populations.⁸⁷ Richkus¹³⁷ hypothesized that high densities of juvenile alewife cropped zooplankton numbers to very low levels and stimulated early emigration of the juveniles to estuarine areas. In landlocked systems such as Lake Michigan, adult alewife are known to feed upon alewife eggs and larvae.^{112,136,182} Cannibalism has also been observed in other landlocked situations;^{78,82} but only two reports of cannibalism in anadromous alewife populations appear in the literature.^{133,134}

Competition with gizzard shad in the Susquehanna River and upper Chesapeake Bay may have contributed to the decline of some alewife populations in Maryland, or is one factor delaying recovery of these stocks. The evidence is purely circumstantial. Carter¹⁵ reported that the catch per effort of gizzard shad in the fish lift at Conowingo Dam on the Susquehanna River steadily increased from 1972 through at least 1981, coincident with the recent period of rapid decline of alewife populations in Maryland.¹⁵⁸

All life stages of the alewife are important forage items for many freshwater and marine fishes, birds, amphibians, reptiles and mammals.⁸⁷ Yellow perch, white perch, spot-tail shiner and other alewife consume alewife eggs.^{37,72} Alewife larvae are consumed by vertebrate and invertebrate predators.²³ Predators on juvenile alewife include American eel and white perch,⁷² grass pickerel, largemouth bass, yellow perch, pumpkinseed,²³ and other fishes.⁸⁷ Kissil⁷³ estimated that one young alewife survived to leave the spawning area of Bride Lake, Connecticut, for every 80,000 eggs spawned. A portion of this high mortality rate during the early life stages may be due to predation. Adult alewife are preyed upon by osprey, green heron, mink,²³ lake trout,¹⁴⁴ Atlantic salmon, striped bass,¹⁵¹ and other fishes.⁸⁷

We could find no information which would implicate predation as a factor which contributed to the general decline of alewife populations in Chesapeake Bay. How-

ever, bluefish and weakfish are two marine piscivores that migrate into the Bay to feed and are known to be predators on alewife.⁴⁰ Data compiled from 1974 through 1986 indicate that the spawning stock biomass of bluefish peaked in 1979, but landings in the Bay were also relatively high from about 1972 through 1986.⁶⁸ Large bluefish were also abundant in the Bay during 1988, from May through mid-October. Weakfish landings in Chesapeake Bay have been below the long-term average in Maryland and Virginia since in the early 1950's.⁶⁸ Nevertheless, combined commercial and recreational landings still totalled 1.6×10^6 kg in 1985. Predation by adult bluefish and weakfish on juvenile alewife during their late summer-fall emigration to the sea could be one factor that is delaying recovery of alewife stocks in Chesapeake Bay.

BLUEBACK HERRING

Food Habits

Juvenile blueback herring tend to be highly planktivorous and feed upon copepods, cladocerans and larval dipterans.^{13,42} In the Cape Fear River, North Carolina, juvenile blueback herring fed principally on small planktonic crustaceans and their eggs.³⁰ An intensive study in Nova Scotian waters observed that microzooplankton, such as calanoid copepods, were the most important food organisms of juvenile blueback herring.^{162,163} Juveniles appear to feed primarily during daylight hours;¹³ however, Loesch⁸⁷ questioned this conclusion.

Food habits of adult blueback herring are poorly documented,⁶⁰ particularly during their spawning runs into fresh water.^{28,41} The stomachs of adults captured in February in offshore North Carolina waters contained several zooplankton groups but no fish.⁵⁴ Spawning blueback herring in the Chowan River, North Carolina, did not stop feeding during their spring migrations to freshwater.²⁸ Nearly all (88%) of the fish sampled in April contained a wide diversity of food organisms that included zooplankters, benthos, terrestrial insects and fish eggs. Females fed more actively than the males and consumed greater numbers of chydorid cladocerans, insects and fish eggs.

Competition and Predation

Few studies have focused on the competitive interactions of blueback herring and other anadromous alosids.⁴⁰ Differences in feeding behavior among juvenile anadromous alosids appear to be a means of avoiding interspecific competitive interactions in nursery areas where they coexist.^{87,92,146} Juvenile blueback herring in the Minas Basin, Nova Scotia, favored smaller and more planktonic prey items than did juvenile alewife.^{162,163} These observed differences in prey selection suggest that juvenile blueback herring are predominantly filter-feeders whereas alewife employ a particulate-feeding strategy. In the Cape Fear

River, North Carolina, juvenile alewife consumed more ostracods, insect eggs and insect parts than did blueback herring.³⁰ Juvenile American shad appear to feed more on terrestrial insects at the surface, less on copepods, and on different cladoceran groups than do juvenile blueback herring.^{31,42} Crecco and Blake²⁷ reported clear differences in the diets of coexisting larvae of American shad and blueback herring in the Connecticut River. They concluded that intraspecific competition for food in these two alosids may be more severe than interspecific competition.

Concerns about introducing blueback herring into closed freshwater systems, particularly when predator stocks are low, include uncontrolled population growth, competition with other fish species for food and space, selective feeding on zooplankton prey, piscivory, and growth of the blueback herring beyond an acceptable prey size for predators.⁸⁷ Few of these potential problems have been observed after the establishment of anadromous runs of blueback herring. From another perspective, Carter¹⁵ observed that the abundance of gizzard shad increased in the Susquehanna River, Maryland, during the same time that river herring populations declined. The ecological connection between these observations, if any, is unclear.

All life stages of blueback herring are important forage items for many freshwater and marine fishes, birds, amphibians, reptiles and mammals.⁸⁷ In freshwater nursery areas and during their seaward migration, juvenile blueback herring are consumed by a variety of predators including eels, striped bass, bluefish, yellow perch, white perch, other fish species, plus reptiles, birds, and mammals.^{87,151} Adult blueback herring are also eaten by marine fish predators and seabirds during the spawning run.¹⁵¹

We could find no information which would implicate predation as a factor which contributed to the general decline of blueback herring populations in the Chesapeake Bay. However, bluefish and weakfish are two marine piscivores that migrate into the Bay to feed and are known to be predators on blueback herring.⁴⁰ Data compiled from 1974 through 1986 indicate that the spawning stock biomass of bluefish peaked in 1979, but landings in the Bay were relatively high from about 1972 through 1986.⁶⁸ Large bluefish were also very abundant in the Bay during 1988, from May through mid-October. Weakfish landings in the Chesapeake Bay have been below the long-term average in Maryland and Virginia since in the early 1950's.⁶⁸ Nevertheless, commercial and recreational landings in both states combined totalled 1.6×10^6 kg in 1985. Predation on juvenile blueback herring by adult bluefish and weakfish during their late summer-fall emigration to the sea could be one factor that is delaying recovery of blueback herring stocks in Chesapeake Bay.

POPULATION STATUS AND TRENDS IN CHESAPEAKE BAY

Records of Commercial and Recreational Landings

Blueback herring and alewife are harvested commercially and recreationally in every Atlantic Coast state except Georgia,¹⁶⁴ and also in the maritime provinces of Canada where they are marketed together as alewife or "gaspereau".^{87,151} In Chesapeake Bay and throughout the U.S. range of these two alosids, they are not distinguished in the records of commercial or recreational landings, but are lumped and reported as alewife or "river herrings". Catches of Atlantic menhaden also may contribute to reported landings of river herrings. In Maryland and Virginia, river herrings are consumed fresh, salted, pickled or smoked; but currently most are used for crab bait, eel bait, pet food and fish meal.^{87,140,145} For a historical perspective on the river herring fishery in Chesapeake Bay and a more detailed discussion of the modern fishery, see Krauthamer and Richkus.⁸¹

Pound nets, gill nets, fyke nets and haul seines are the primary commercial gear for catching river herrings in Chesapeake Bay.^{168,158} Detailed descriptions of the dimensions of typical pound nets used in the Patuxent River, the Susquehanna Flats/Head of Bay region, and Fishing Bay, Maryland, are provided in Mowrer *et al.*¹¹⁶ Virginia historically has taken the largest portion of the total Chesapeake Bay harvest.¹⁴⁰

Substantial offshore landings of river herrings were reported by foreign fishing fleets operating in U.S. coastal waters between 1967 and 1972.¹⁵⁸ Since 1973, river herring catches by foreign fleets have been relatively low because of agreements between the U.S. and foreign countries and enactment of the 200-mile limit.¹ In recent years, the by-catch of river herrings in the offshore Atlantic mackerel fishery has become a growing concern to resource managers in Maryland and Virginia.¹⁸ This fishery is composed of a joint-venture fishery and a directed fishery by foreign vessels. By-catch of river herrings is variable from year to year, averaged about 48×10^3 kg between 1981 and 1989 and appears to be increasing.⁴⁶ By-catch limits for river herrings in the offshore mackerel fishery are currently set at 100×10^3 kg.

Maryland and Virginia are working to ensure that river herring by-catch in the offshore mackerel fishery is minimized.¹⁸ Both states are monitoring river herring by-catch and support recommendations from the Mid-Atlantic Fishery Management Council that the foreign fishery stay at least 20 miles offshore, that a maximum by-catch of river herrings be maintained and enforced, and that intercept fisheries be discouraged.

Sport fishermen take river herrings with dip nets and by hook and line in Maryland and Virginia during the spring spawning runs; dip nets are the primary gear.⁸¹ Recreational exploitation of river herrings was widespread along the banks of the Susquehanna River, upper Bay area, and the Choptank, Nanticoke and Potomac Rivers of Maryland during the 1960's. Dip netting was so popular at some locations that space to dip was often difficult to find on March and April nights when the spawners were running.⁸¹ The recreational dip net fishery for river herring decreased sharply in the early 1970's in Maryland waters. River herring are still landed with dip nets, but are often incidental catches to the targeted species, white perch. Daily catches of river herrings by dip net fishermen in Virginia during 1977 and 1978 ranged from 30-40 fish per fisherman, depending upon time and site.⁹⁴ These spotty reports suggest that annual catches of river herrings by sport fishermen may have been and still may be substantial; unfortunately, accurate records of recreational catch and effort are not available for Chesapeake Bay. This source of mortality on alewife and blueback herring adults should be measured, given the declining trends in stock abundance that began in the 1970's and have not yet improved.

Of all the anadromous fish species harvested in the Chesapeake Bay, the river herrings experienced the most drastic decline in commercial landings.¹⁵⁸ Reported landings in Maryland and Virginia totalled 9.5×10^6 kg as recently as 1970; by 1980, landings dwindled to 0.6×10^6 kg.¹⁴⁰ Recent landings are the lowest ever recorded by either state and reflect a similar decline in all river systems.⁸¹ The proportion of blueback herring to alewife increased during the 1970's, concomitant with a reduction in commercial landings, suggesting that the rate of decline in alewife stocks exceeded the rate of decline in blueback herring stocks.¹⁴⁰ A portion of the overall decline in river herring landings may be related to a reduction in pound net fishing effort between 1929 and 1980.¹⁴³ However, the magnitude of the reduction in reported landings in the Bay cannot be completely accounted for by a reduction in pound net effort alone,¹⁴⁰ and also must reflect a real decline in stock abundance. The population estimate of river herring stocks in the Susquehanna River for 1980 (93,585) suggested an abundance decline of at least an order of magnitude since 1961.^{39,81}

Juvenile Abundance Indices

Virginia and Maryland conduct annual juvenile surveys in alewife and blueback herring nursery areas in an effort to develop annual indices of reproductive success.^{8,81,140,158} Indices from both States have sampling design features that limit their abilities to estimate juvenile alewife or blueback herring production accurately every year. The juvenile indices likely can discriminate very good from very poor year classes. These indices suggest that alewife are generally less abundant than blueback herring. Recent

trends in juvenile alewife and blueback herring abundance are down in all river systems of both states,¹⁴¹ even though the apparent decline in some rivers cannot be statistically confirmed.⁸¹

Current Status of Spawning Populations in the Major Bay Tributaries

A qualitative assessment of the current status of alewife and blueback herring spawning populations in each of the major tributary systems to Chesapeake Bay is presented in this section. For another perspective on the current status of river herring stocks in Chesapeake Bay that generally agrees with ours, see Richkus *et al.*¹⁴¹ Our assessment was drawn from recent surveys,^{7,8,44,45,55,59,87,88,89,90,91,93,123,178,179} the observations of fisheries biologists associated with these surveys, and other informed individuals (personal communications: Larry Leasner, James Mowrer, Jay O'Dell and Harley Speir, Maryland Department of Natural Resources; Herb Benjamin, Northeast, Maryland; Joice Davis, Joseph Loesch, and James Owens, Virginia Institute of Marine Science). This assessment is relevant to the 1980's, especially the latter half of this decade, and represents a perspective on the current spawning populations compared to conditions in the late 1960's when Baywide alewife and blueback herring populations were much more abundant than they are today.

ALEWIFE

Susquehanna River

Deer Creek: a remnant population that is at a very low level of abundance.

Octoraro Creek: a remnant population that is at a very low level of abundance.

Bush River

A remnant population that is at a very low level of abundance, but appears to be stable.

Gunpowder River

A remnant population that is at a low level of abundance, but appears to be stable.

Patapsco River

Probably no more than a very small remnant population left.

Magothy River

Probably none left.

Severn River

A remnant population that is at a low level of abundance.

South River

A remnant population that is at a low level of abundance.

West River

Probably no more than a small remnant population left.

Patuxent River

A remnant population that is at a low level of abundance, but appears to be stable.

Potomac River

St. Mary's River: none, alewife probably never have spawned there.

Breton Bay: none, alewife probably never have spawned there.

St. Clements Bay: none, alewife may never have spawned there.

Wicomico River: probably none left.

Port Tobacco River: probably none left.

Nanjemoy Creek: a remnant population that appears to be declining.

Mattawoman Creek: a moderately abundant population that appears to be stable.

Piscataway Creek: a remnant population that appears to be stable.

Anacostia River: probably none left.

Rock Creek: a remnant population that appears to be stable.

Rappahannock River

A population that is at a low level of abundance, but appears to be stable.

York River

Mattaponi River: a population that is at a low level of abundance, but appears to be decreasing.

Pamunkey River: a population that is at a low level of abundance, but appears to be stable.

James River

Current status of this population is not known.

Chickabominy River

The catch records of river herring (alewife not separated from blueback herring) suggest that there is an abundant population of mostly blueback herring.

Pocomoke River

A remnant population that appears to be declining; probably was never very abundant.

Nanticoke River

A moderately abundant population that may be increasing.

Honga River

Probably none left.

Choptank River

A remnant population that is at a very low level of abundance and may be declining.

Wye River

Probably none left.

Chester River

A remnant population that is at a low level of abundance and may be declining.

Sassafras River

A remnant population that is at a very low level of abundance.

Bohemia River

A remnant population that is at a very low level of abundance.

Elk River

A remnant population that is at a very low level of abundance and may be declining.

Northeast River

A remnant population that is at a low level of abundance and may be declining.

BLUEBACK HERRING

Susquehanna River

Deer Creek: a remnant population that appears to be declining.

Octoraro Creek: a remnant population that appears to be declining.

Bush River

A remnant population that is at a very low level of abundance.

Gunpowder River

A remnant population that is at a low level of abundance and appears to be declining.

Patapsco River

A remnant population that appears to be stable at a very low level of abundance.

Magothy River

Probably none left.

Severn River

A remnant population that is at a low level of abundance.

South River

A remnant population that is at a low level of abundance.

West River

Probably no more than a very small remnant population left.

Patuxent River

A remnant population that appears to be stable.

Potomac River

St. Mary's River: probably none, blueback herring may never have spawned there.

Breton Bay: probably none, blueback herring may never have spawned there.

St. Clements Bay: probably none, blueback herring may never have spawned there.

Wicomico River: a remnant population that is at a very low level of abundance.

Port Tobacco River: a remnant population that is at a very low level of abundance.

Nanjemoy Creek: a remnant population that appears to be declining.

Mattawoman Creek: a moderately abundant population that appears to be stable.

Piscataway Creek: a remnant population that appears to be stable.

Anacostia River: a remnant population that appears to be stable.

Rock Creek: probably none left.

Rappahannock River

Moderately abundant population that appears to be stable.

York River

Mattaponi River: a moderately abundant population that may be decreasing.

Pamunkey River: a moderately abundant population that appears to be stable.

James River

Current status of the blueback herring population is not known.

Chickahominy River

The catch records of river herring (alewife not separated from blueback herring) suggest that there is an abundant population of mostly blueback herring.

Pocomoke River

A remnant population that appears to be declining.

Wicomico River

A remnant population that appears to be declining.

Nanticoke River

A moderately abundant population that appears to be increasing.

Honga River

A remnant population that appears to be declining.

Choptank River

A moderately abundant population that appears to be stable.

Wye River

Probably none left.

Chester River

A population that is at a low level of abundance but appears to be stable.

Sassafras River

A remnant population that is at a very low level of abundance.

Bohemia River

A remnant population that is at a very low level of abundance.

Elk River

A remnant population that is at a low level of abundance but appears to be increasing.

Northeast River

A remnant population that appears to be declining.

HABITAT REQUIREMENTS

ALEWIFE

Much of the research focused on the specific environmental requirements of the alewife dealt with landlocked populations. Less effort has been expended on anadromous populations. The information presented below

does not distinguish the findings of landlocked from migratory alewife studies.

Temperature

Temperature effects on alewife eggs were investigated in several studies. The initial research on the effects of once-through power plant exposures on alewife eggs was conducted by Schubel and Auld.^{148a} Eggs were acclimated at 17°C and then exposed to 24.5°C conditions for 6-60 minutes. No significant differences in hatching success were reported, nor was there any evidence of abnormal egg development. In a similar experiment with alewife eggs, the acclimation temperatures ranged from 12-14.5°C, whereas test temperatures remained between 18 and 24.5°C.¹⁴⁷ No significant difference in hatching success was noted among the various time-temperature treatments.

Koo *et al.*^{80a} exposed alewife eggs to temperature increases of 10-14.5°C for 5 and 15 minutes. A 15 minute exposure at 28.4°C resulted in significantly greater egg mortality than was observed in the controls. A five minute exposure at 35.6°C did not significantly reduce egg survival. A critical thermal maximum (CTM) temperature of 35.6°C was reported for alewife eggs acclimated at 20.6°C.^{80b} The critical exposure period was 5-10 minutes at the CTM.

An optimum hatching temperature of 17.8°C for alewife eggs was reported by Edsall.³⁸ Some hatching occurred over the range of 6.9-29.4°C. But, at incubation temperatures below about 11°C, 69% of the newly-hatched larvae were deformed. In another laboratory study, maximum hatching success of alewife eggs occurred at 20.8°C; no eggs hatched at 29.7°C.⁷¹ Time of median hatch was inversely related to temperature: 7.4 days at 12.7°C and 3 days at 26.8°C. Alewife eggs were collected at water temperatures ranging from 7-14°C in the upper Chesapeake Bay; 70% were collected between 12-14°C.³⁴

The effects of temperature on alewife larvae also have been studied. Larvae acclimated at 16.4°C tolerated a 15 minute exposure to temperatures ≤ 30.9°C.^{80a} Koo *et al.*^{80b} later reported that larvae survived a one-hour exposure at 33.6°C when acclimated to 18.6°C. The preferred temperature range for alewife larvae acclimated at 20°C was 23-29°C.^{36,71} An upper temperature tolerance limit of 31°C was reported for yolk-sac larvae acclimated at 14-15°C.⁷¹ Growth rates of alewife larvae were considerably lower when they were reared in freshwater compared to saltwater (1.0-1.3 ppt) at 26.4°C. Small temperature increases above 20.8°C resulted in substantial growth increases. Larval and juvenile alewife were collected at water temperatures between 4 and 27°C in the upper Chesapeake Bay; 98% were collected at 25°C.³⁴

Temperature effects on juvenile alewife were observed by Jude *et al.*⁷⁰ and Brandt *et al.*¹⁰. They reported that juveniles were most abundant at temperatures > 17°C during the day in Lake Michigan. Juvenile alewife appear to avoid temperatures above 25°C.¹³⁰ Optimal temperatures are considered to be 15–20°C. The preferred temperature range for juvenile alewife was 17–23°C at 4–7 ppt salinity when they were acclimated at 15–21°C.^{106,134} A final temperature preferendum of 19.5°C for juveniles acclimated at 20°C and a 96 h LC₅₀ temperature of 32.6°C for juveniles acclimated at 25°C was reported.³⁶ No mortality occurred when juveniles were exposed to 9°C, following acclimation at 20°C in 5.5 ppt salinity.¹³⁴ However, 27–60% mortality was observed when they were exposed to 7°C for 96 h. Significant mortality was observed at 30–31°C for juveniles acclimated at 16.2°C.¹⁶⁰ A 20% survival rate was observed for juveniles that were exposed for 24 h to 35°C after acclimation at 18.9–20.6°C.³³ The results were similar when juveniles were acclimated to 19 and 22°C at 6 ppt salinity before exposing them to 28.5°C.¹³⁴ The 22°C acclimation group experienced 20% mortality after 24 h of exposure, while the 19°C group experienced 25% mortality after 96 h. Juvenile alewife acclimated to 17, 18, and 25°C in 4.0–4.5 ppt salinity avoided temperatures of 26, 24 and 30°C, respectively.¹⁰⁵ Juveniles acclimated to 26°C avoided temperatures ≥ 34°C.¹³⁴

The upper incipient lethal temperature for juvenile alewife acclimated to 9°C was 23°C.⁴³ Otto *et al.*¹²⁹ collected wild juveniles and adults during the summer and then compared upper incipient lethal temperature limits after acclimation to 10, 20 and 25°C. They reported upper lethal temperatures for juveniles that ranged from 26.5–32.1°C. These upper lethal temperatures were 3–6°C higher than those for adult alewife. Preferred temperatures for juvenile alewife (24–25°C in summer, 19–21°C in winter) were consistently higher than those of adults (16–21°C in summer, 11–16°C in winter).¹²⁹ Juveniles suffered greater than 90% mortality when exposed to decreasing temperatures (15.6–2.8°C) over a 15-day period.²³

Several other studies examined the effects of temperature on adult alewife. Marcy¹⁰⁰ collected adults from a discharge canal along the Connecticut River when temperatures ranged from 5.7–31.0°C. Adult alewife were most abundant at depths in Lake Michigan where water temperatures ranged from 11–16°C during the day.^{10,180} However, in another study, adults were most abundant at depths where temperatures ranged from 16–22°C.⁷⁰ Alewife recruitment, abundance and distribution in the Great Lakes were influenced by water temperature.⁴⁹ An upper temperature preferendum of 21.3°C was observed for adults collected during the spring from Lake Erie and tested in the laboratory.¹³⁵ Adults avoided 26 and 30°C when acclimated at 16 and 20°C.³⁶ Wells¹⁸⁰ reported

upper and lower avoidance temperatures of 22.0 and 8.0°C for adult alewife in Lake Michigan.

Upper incipient lethal temperatures ranged from 23.5–24.0°C when adult alewife were acclimated to 10, 20 and 25°C.¹²⁹ These results were similar to those of Graham.⁴³ However, Stanley and Holzer¹⁶¹ reported upper incipient lethal temperatures of 29.8 and 32.8°C for adults acclimated to 16.9 and 24.5°C, respectively. Similarly high upper incipient lethal temperatures (31–34°C) were estimated for adults acclimated at 27°C.¹⁰³ Mortalities observed in adult alewife exposed to 16 ± 10°C were not directly related to temperature, but rather to increased fungal infection.¹⁶¹

The lower incipient lethal temperature range for adult alewife acclimated to 15.0 and 21.0°C lies between 6 and 8°C; the ultimate lower lethal temperature is about 3°C.¹²⁹ Adult alewife acclimated to 21°C exhibit 30% mortality when subjected to 10.5°C.¹²⁹ Mortality increased to 40 and 91% when these adults were subjected to 8.0 and 7.0°C.

Dissolved Oxygen

A paucity of information exists regarding the sensitivities of various life history stages of alewife to dissolved oxygen (DO). Minimum DO concentrations are 5.0 mgL⁻¹ for eggs and larvae and 3.6 mgL⁻¹ for juveniles and adults.⁶⁸ Juvenile alewife in the Cape Fear River system, North Carolina, selected areas where DO ranged from 2.4–10.0 mgL⁻¹.³⁰ Dorfman and Westman³³ observed 33% mortality for adult alewife exposed to DO ranging from 2.0–3.0 mgL⁻¹ for 16 h in the laboratory. They also reported that adults could survive exposure to DO as low as 0.5 mgL⁻¹ for up to five minutes if access to an area with DO > 3 mgL⁻¹ was available. The test fish responded to DO below 2.0 mgL⁻¹ by moving toward the surface of the test chambers.

Salinity

An unstressed anadromous alewife is apparently an excellent ion regulator and quite tolerant of wide salinity changes;²⁵ however, experimental evidence to support this view is limited. Richkus¹³⁷ reported zero mortality when adult and juvenile alewife were either transferred directly from fresh water to saline water (32 ppt) or vice versa.

Concentrations of the electrolytes sodium, potassium, and calcium in blood and muscle tissue of adult alewife held in sea water and fresh water were similar, indicating that after a period of acclimation, the alewife were efficient osmoregulators in either environment.¹⁶⁰ However, when alewife were exposed to decreasing temperatures (from 16 to 3°C at a rate of 2.5°C per day), a cold-induced ionic imbalance was observed. They concluded that alewife mortalities in the Great Lakes might be related to ionic

imbalance resulting from acute exposure to cold but not warm temperatures.

Alewife eggs were collected in areas of the upper Chesapeake Bay where salinities ranged from 0-2 ppt; 99% of the eggs were collected in strictly fresh water.³⁴ Larvae and juveniles were collected in areas that ranged from 0-8 ppt; 98% were collected between 0-3 ppt and 82% were collected in fresh water. Pardue¹³⁰ concluded that salinities of 5 ppt or less were optimal for alewife.

pH

We could find only a limited amount of laboratory and field data on the sensitivity of various life history stages of alewife to pH.

Adults were able to tolerate pH changes as large as 0.8 unit within a range of pH 6.5-7.3.²⁴ Byrne¹⁴ measured a median pH of 5.0 in several New Jersey coastal plain streams that still had alewife but not blueback herring spawning runs. His observations suggested that the early life stages of alewife were able to tolerate more acidic conditions in those waters than blueback herring. Based on static-renewal toxicity tests conducted in the laboratory using water from four acidic impoundments (pH 4.5-5.3), he also suggested that successful spawning of alewife in those streams could occur at pH as low as 4.5. Juvenile alewife from the Cape Fear River system, North Carolina, were collected in areas where free carbon dioxide ranged from 4-22 mgL⁻¹ and pH ranged from 5.2-6.8.³⁰

Klauda⁷⁴ proposed critical acidity conditions (defined as laboratory and field exposures associated with > 50% direct mortality) for alewife reproduction in Maryland coastal plain streams based upon data available for the congeneric blueback herring. Critical conditions for alewife reproduction could occur during an acidic pulse between pH 5.5 and 6.2 with concomitant concentrations of total monomeric aluminum ranging from 15-137 µgL⁻¹ for a pulse duration of 8-96 h. In a recent laboratory experiment with alewife (Klauda *et al.* unpublished), yolk-sac larvae appeared to be relatively tolerant of the single 12 and 24 h acid and aluminum pulses that were tested. Alewife larvae tolerated a single 24 h, acid-only pulse to pH 4.5 with no mortality, and a single 12 h, acid-only pulse to pH 4.0 with 38% mortality. Larval mortality increased to 96% during a 24 h exposure to a single pH 4.5 pulse accompanied by a 446 µgL⁻¹ pulse of inorganic monomeric aluminum.

Hardness and Alkalinity

We could find no information on water hardness or alkalinity optima or tolerances for any life history stage of alewife (see **Salinity** subsection). Davis and Cheek³⁰ collected juvenile alewife in areas of the Cape Fear River system, North Carolina, where alkalinities ranged from 5-32 mgL⁻¹.

Suspended Solids

The effects of suspended solids on alewife eggs were examined in the laboratory,¹⁴⁹ but the experiment was terminated prematurely due to an extensive fungal infestation. They concluded that high levels of sediment could increase infection rates of eggs in natural environments. In a later study, alewife eggs exposed to concentrations of suspended solids ranging from 50-1000 mgL⁻¹ showed no significant reduction in hatching success.³

Current Velocity and Turbulence

We could find no information on current velocity and turbulence optima or tolerances for any life history stage of alewife. Successful spawning has been documented over a wide range of velocity conditions from standing water to fast-flowing streams.⁶⁷

Physical Habitat

Alewife spawn in a diversity of physical habitats that includes large rivers, small streams and ponds, over a range of substrates such as gravel, sand, detritus, and submerged vegetation and in areas with sluggish water flows and depths ranging from about 0.2-3 m.^{25,87,121,130} Substrates with 75% silt or other soft materials containing detritus and vegetation and sluggish flows were considered by Pardue¹³⁰ to be optimal for providing cover for spawning river herring and their eggs and larvae. We could find no information on physical habitat requirements for any other life history stage of alewife.

BLUEBACK HERRING

Some research has been conducted on the specific environmental requirements of river herrings. Most of this work was focused on landlocked populations of alewife (summarized above in the ALEWIFE section). Information specific to blueback herring is presented below.

Temperature

Temperature effects on blueback herring eggs were investigated in several studies. Blueback herring eggs were collected in waters with temperatures ranging from 7-14°C in upper Chesapeake Bay; 90% were collected at 14°C.³⁴ No significant reduction in hatching success was reported for eggs acclimated at 15-18.3°C and exposed to temperatures of 22-28.3°C for 5-30 minutes in the laboratory.¹⁴⁷ No significant reduction in hatching success was reported for eggs acclimated at 17.9-21.1°C and then exposed to 31.1°C for 0.5 h.^{148b} However, a significant reduction in hatching success occurred when blueback herring eggs were exposed to temperatures of 32.9-36.1°C for 5-15 minutes; total egg mortality occurred at 37.9°C.

One laboratory study evaluated the effects of temperature on blueback herring eggs and larvae collected from a population in New Brunswick. Fertilized eggs were exposed to 29 and 34°C for 60-180 minutes after acclimation to 19°C.⁷⁹ Egg mortality and hatchability were not good

indicators of temperature effects. The severity of larval deformity, however, was directly related to exposure temperature and duration; 100% deformity occurred in larvae exposed to 34°C for three hours. Deformities were permanent, ranged from minor curvature of the spine to complete lack of normal larval form and behavior and would have decreased larval survival. Dovel³⁴ collected larval and juvenile blueback herring in waters with temperatures of 13-28°C; 96% were collected at 23-28°C.

In laboratory studies, juvenile blueback herring acclimated to 25 and 26°C in 7-8 ppt salinity preferred temperatures ranging from 24-28°C.¹³⁴ Marcy and Jacobson¹⁰¹ acclimated juveniles at 19 and 22.7°C before exposing them to 32-33°C. Mortality rates after four to six minutes of exposure for the 19 and 22.7°C acclimation groups were 100 and 61.7%. Juveniles acclimated at 15°C suffered 100% mortality after a six minute exposure to 30.5°C.¹³⁴ Juveniles acclimated at 25°C in 6.5-7 ppt salinity survived exposure at 12-13°C, but suffered total mortality when exposed to 10°C.¹³² Juveniles acclimated at 5°C in 8.5-10 ppt salinity survived at 3°C, but suffered 100% mortality at 0.2°C.

An avoidance temperature of 36°C was reported for juveniles acclimated to 26°C and 7 ppt salinity.¹³² Juvenile blueback herring acclimated at 16°C and 29 ppt salinity avoided 26-28°C conditions.¹⁶⁹ These investigators also acclimated juveniles at 15°C and 29 ppt salinity prior to exposure to 20, 25 and 32°C. No mortality was observed during exposures to 20 and 25°C, but total mortality occurred within six minutes when the fish were exposed to 32°C. In laboratory tests, preferred (selected) temperatures of young blueback herring (ages 0+ and I+) collected from the Delaware River, New Jersey, ranged from 20-22°C at salinities of 4-6 ppt and acclimation temperatures of 15-21°C.¹⁰⁶ Juvenile and adult blueback herring were collected from a discharge canal along the Connecticut River at water temperatures of 6.7-32.5°C.¹⁰⁰ Juveniles were captured in the Cape Fear River, North Carolina, when water temperatures ranged from 11.5-32°C.³⁰

Pardue¹³⁰ concluded that optimum spawning temperatures for blueback herring adults were 20-24°C. A single laboratory experiment with adults reported that fish acclimated to 15°C and 29 ppt salinity exhibited a final temperature preferendum of 22.8°C.¹⁶⁹

Dissolved Oxygen

We could find no information on dissolved oxygen (DO) optima or tolerances for blueback herring eggs. The larvae and adults require DO of at least 5.0 mgL⁻¹.⁶⁷ Adults were never captured at sampling stations in the Cooper and Santee Rivers, South Carolina, where DO levels were less than 6 mgL⁻¹.²¹ A minimum DO of 3.6 mgL⁻¹ is required for juveniles. Dorfman and Westman³³ reported 33% mortality for juveniles exposed to DO of 2.0-3.0 mgL⁻¹ for 16

h. The juveniles were unable to detect and avoid waters with low DO. Juveniles in the Cape Fear River, North Carolina, were collected in areas where DO ranged from 2.4-10.0 mgL⁻¹.³⁰ Mass mortalities of juvenile blueback herring occurred in the lower Connecticut River during summer (June and July) in 1965, 1966, 1967 and 1971. Mortalities were most evident in the early morning when DO was below 3.6 mgL⁻¹ and the water temperature was 27.6°C.¹¹³

Salinity

The eggs, larvae, juveniles and adults of blueback herring are tolerant of a wide range of salinities. Live eggs, yolk-sac larvae and postlarvae were collected in a Canadian coastal stream where salinities reached 22 ppt.⁶⁶ When Chittenden^{19b} transferred wild juveniles directly from fresh water to 28 ppt at 22°C, only one of the 10 juveniles died (at nine hours post-transfer) during the six day observation period following the transfer. Handling stress probably was related to the observed mortality. Spawning can occur in waters with 0-6 ppt salinity; but most spawning activity occurs in waters with less than 1 ppt. Juveniles tend to inhabit waters of 0-2.0 ppt prior to their fall migrations to the sea.⁶⁸ Adult blueback herring were collected at 0-35 ppt. Pardue¹³⁰ concluded that optimal salinities for blueback herring are less than 5 ppt.

pH

Based on a series of laboratory experiments with fertilized eggs and yolk-sac larvae, Klauda⁷⁴ proposed that critical acidity conditions (defined as laboratory and field test exposures associated with > 50% direct mortality) for successful blueback herring reproduction in Maryland coastal plain streams occur during a single 8-96 h pulse of acid, pH 5.5-6.2, with concomitant total monomeric aluminum concentrations of 15-137 µgL⁻¹. Klauda *et al.*⁷⁷ reported a pH-induced mortality threshold for yolk-sac larvae of pH 5.7-6.5, and a 96 h LC₅₀ pH of 6.37 (pH that killed 50% of the test organisms during a laboratory study), with no aluminum present. Highly variable mortality rates for yolk-sac larvae (3-75%) were observed at pH 6.7. The mortality rate for larvae nearly doubled (25-49%) as the duration of exposure to a single acid pulse of pH 5.5 with no aluminum doubled from 12 to 24 hours (Klauda and Palmer 1987a). They also reported 19% mortality when blueback herring yolk-sac larvae were exposed for four hours to a pH minimum of 5.5 and total aluminum maxima of 100-150 µgL⁻¹. Mortality increased to 66, 98 and 100% as exposure increased to 8, 12 and 24 h, respectively.⁷⁵ Yolk-sac larvae were more sensitive than four-hour old embryos to pH and aluminum treatments.⁷⁶ Their laboratory data indicated that larvae were adversely affected by pH 5.7 and 6.2, when no aluminum was added, but seemed to tolerate pH 6.7 and 7.5. The time period over which larval blueback herring succumbed to exposures to pH 5.7 and 6.2 was significantly reduced

with the addition of 200-400 $\mu\text{g/L}^{-1}$ of aluminum to the acid treatments.^{76,77}

Klauda and Palmer⁷⁶ also investigated the effects of four acid treatments (pH 5.7-7.5) and five aluminum treatments (0-400 $\mu\text{g/L}^{-1}$ nominal) during several 96-120 h continuous exposure laboratory experiments with blueback herring eggs. Only four-hour old embryos were sensitive to aluminum in the test treatments of pH 5.7-6.7. Twelve-hour old embryos were most sensitive to pH 5.7 with no aluminum. The oldest embryos tested (24 h) were resistant to all pH and aluminum levels.

We could find no information on pH optima or tolerances for juvenile or adult blueback herring. Davis and Cheek³⁰ collected juveniles from areas of the Cape Fear River, North Carolina, where pH ranged from 5.2-6.8. Time spent by the juveniles in any portion of this pH range was not reported. Adult blueback herring were never captured at sampling stations in the Santee-Cooper River system, South Carolina, where pH was less than 6.0 or greater than 7.5.^{20,21} Byrne¹⁴ investigated river herring spawning runs in the tailwaters of 27 impoundments on Delaware River tributaries in New Jersey. Blueback herring runs occurred at only eight study sites. Monthly pH measurements at these eight sites during April, May and June ranged from pH 4.7-7.1 (mean 6.2).

Hardness and Alkalinity

We could find no information on water hardness and alkalinity optima or tolerances for any life history stage of blueback herring (see **Salinity** subsection). Juveniles were collected in areas of the Cape Fear River system, North Carolina, where alkalinity ranged from 5-32 mg/L^{-1} .³⁰

Suspended Solids

Concentrations of suspended solids $\leq 1000 \text{ mg/L}^{-1}$ did not significantly reduce hatching success of blueback herring eggs.³ High levels of suspended solids during and after spawning may significantly increase rates of egg infections from naturally occurring fungi¹⁴⁹ and cause delayed mortalities.

Blueback herring larvae appear to be more sensitive to suspended solids than the egg stage. During field tests with yolk-sac larvae in Lyons Creek, Maryland, Klauda and Palmer⁷⁶ observed that a storm-induced turbidity maximum of 450 NTU (estimated suspended solids concentration 830 mg/L^{-1})¹¹ was associated with 100% mortality of the larvae during a four-day *in situ* test. Mortality of blueback herring larvae also was positively correlated with turbidity during other four-day *in situ* tests in three Maryland coastal plain streams.⁴⁵ Total larval mortality was observed during field tests that coincided with rain events and encountered maximum stream turbidity levels of 47-198 NTU. However, because storm-induced changes in stream turbidity also were associated with changes

in stream pH and current velocity, the effects of turbidity, by itself, on larval survival could not be discriminated by these *in situ* tests.

Current Velocity and Turbulence

We could find no information on current velocity and turbulence optima or tolerances for any life history stage of blueback herring.

Physical Habitat

Blueback herring spawn in a diversity of physical habitats that include relatively fast flowing sections of freshwater tributaries, channel sections of fresh and brackish tidal rivers, Atlantic coastal ponds, seasonally flooded rice fields, cypress swamps, and oxbows.^{41,87,130} Pardue¹³⁰ concluded that substrates with 75% silt or other soft materials containing detritus and vegetation and sluggish flows are considered optimal to provide cover for spawning river herring and their eggs and larvae. We could find no information on physical habitat requirements for any other life history stage of blueback herring.

SPECIAL PROBLEMS

ALEWIFE

Contaminants

Relatively little information exists on the acute and chronic effects of contaminants on any life history stage of the alewife. A 24 h LC_{50} of 2.25 mg/L^{-1} for total residual chlorine (TRC) was reported for juveniles exposed for 30 minutes at 10°C.¹⁵³ Thirty-minute LC_{50} values for TRC were 2.27 mg/L^{-1} for juveniles exposed at 10°C, and 0.30 mg/L^{-1} when the fish were exposed at 30°C.^{12,152} Juvenile alewife held at 15°C in 7 ppt salinity exhibited an avoidance response to 0.06 mg/L^{-1} TRC.¹³² An avoidance response occurred at $< 0.03 \text{ mg/L}^{-1}$ TRC for juveniles held in fresh water at 19 to 24°C.⁹

Nutrients

We could find no information which would directly implicate high nutrient levels as a factor contributing to the general decline of alewife populations in Chesapeake Bay or preventing stock recovery. Rulifson *et al.*¹⁴⁵ mentioned low DO, sewage outfalls and poor water quality as nutrient-related factors that were "possibly important or very important in contributing to the decline of certain populations of alewife" in North Carolina.

In an interesting study, Limburg and Schmidt⁸⁵ observed a significant negative correlation ($r^2=0.732$) between densities of anadromous fish eggs and larvae (93% alewife) produced in tributaries to the Hudson River, New York, and an index of urbanization in the watersheds of these tributaries. When the percent of a watershed in urban land usage increased to about 10%, egg and larval densities in the associated tributaries declined sharply. They also reported that DO saturation declined to about 70-80%

during the alewife spawning and early nursery period (April-June) in those study streams that were near urban centers. A negative relationship between DO saturation and percent of watershed area in urban land uses was apparent in their study streams.

Nutrient inputs to Chesapeake Bay and its tributaries from point sources, stormwater runoff, groundwater and atmospheric deposition are of concern to scientists and resource managers. Excessive nutrient enrichment stimulates heavy growths of phytoplankton. Death and decay of phytoplankton blooms involve high rates of dissolved oxygen consumption which can lead to low DO during the growing season in the bottom layers of the Bay's deeper channels, and to diurnally low DO in tidal tributaries.^{26,171} These conditions can stimulate fish kills during hot summer months. Nutrient reduction is a major goal of the 1985 Chesapeake Bay Restoration and Protection Plan.^{29,159} Achieving nutrient reduction goals should increase DO in alewife nursery areas and in the mainstem Bay, and perhaps help to stimulate recovery of alewife stocks throughout Chesapeake Bay.

Parasites and Diseases

Few studies of parasites or diseases of alewife have been published.¹⁵¹ Several parasites were collected from alewife taken near Woods Hole, Massachusetts, and included an acanthocephalan, a cestode, four trematodes and three copepods.¹⁶⁸ Piscine erythrocytic necrosis (PEN), a blood disease, was reported in anadromous alewife collected from coastal Maine waters.¹⁵⁴ We could find no information which would implicate parasites or diseases as factors which contributed to the general decline of alewife populations in Chesapeake Bay or are preventing stock recovery.

Impediments to Spawning Migrations

Man-made dams, impoundments, stream flow gauging weirs, roadway culverts, bridge aprons and natural impediments to fish spawning migrations such as beaver dams, water falls and log/debris piles have been suggested as factors which may have contributed to the decline of alewife populations in Maryland and Virginia.^{1,158} Man-made dams currently block alewife spawning runs on mainstem segments of several major river systems including the Susquehanna, Patapsco, Patuxent, Potomac, Rappahannock, Chickahominy, Appomattox and James (Map Appendix). The role of man-made dams and impoundments in alewife stock declines is uncertain. No dams have been constructed on any major Bay tributary since the mid-1940's, long before the major stock declines of the late 1960's to mid-1970's began. Impediments to spawning migrations also exist on many smaller tributaries to the Chesapeake Bay.¹⁷

During a 1970-1971 survey of anadromous fish spawning areas in the Potomac River system, O'Dell *et al.*¹²² docu-

mented 44 constructed barriers on 27 streams, 53 beaver dams on 11 streams, 17 waterfalls on eight streams, and 185 log/debris piles on 41 streams that either completely blocked access to spawning fish migrations or permitted fish passage only during high water levels. Plans for fish passage facilities at Little Falls Dam on the mainstem Potomac River near the District of Columbia, and at Pierce Mill Dam on Rock Creek in the District of Columbia are in the serious discussion stage.¹⁷

A similar stream survey was conducted in the Patuxent River system between 1980 and 1983.¹²³ Seventy-six man-made structures on the mainstem and 144 on tributaries were documented that had the potential to block alewife spawning runs. Man-made structures included dams, stream flow measuring weirs, roadway culverts, bridge aprons and pipeline crossings. There were 178 natural barriers (waterfalls, beaver dams, log/debris piles) documented which could block or impede spawning runs.

A conceptual design for a fish passage structure to be constructed at the Fort Meade Dam (at Maryland Rte. 198 bridge) on the Little Patuxent River was developed by the U.S. Fish and Wildlife Service in conjunction with the U.S. Department of the Army and MDNR. A denil-type fish ladder was completed at this site in March 1991. This fish passage facility at the Fort Meade Dam will open up almost 13 km of potential spawning habitat to alewife. Stream surveys also were conducted in major river systems on Maryland's eastern shore.^{55,178,179}

The Patapsco River in Maryland presently is blocked by four dams: Bloede, Simpkins, Union and Daniels. All dams except Simpkins are State-owned and located in Patapsco State Park.¹⁷ Simpkins Dam is an industrial water supply dam owned by Simpkins Industries. Maryland DNR, cooperating Federal agencies, and the Chesapeake Bay Foundation (CBF) have developed engineering plans for fish ladders at the Bloede and Daniels dams. A plan developed with Howard County calls for removal of a portion of Union Dam to create fish passage opportunities. Simpkins Industries is expected to fund a fish passage structure for their water supply dam. Actions also are proceeding to remove three blockages on two tributaries to the Patapsco River: Stoney Run and Deep Creek.

A town water supply dam in Elkton, Maryland, on Big Elk Creek, recently was targeted as a demonstration fish passage project in a cooperative effort among MDNR, CBF and the Town of Elkton.¹⁷ Funds provided by MDNR will be used to construct a fish ladder that should begin construction in late 1991. When completed, the Elkton fish ladder will restore 16-24 km of potential spawning habitat for alewife in Big Elk Creek.

Discussions held between MDNR and U.S. Army officials concerning the construction of fish passage facilities on Winters Run in the Bush River drainage were successful. A denil-type fish ladder was completed in August 1990 and began functioning during the spring 1991 spawning season. New fish passage facilities also are planned for Susquehanna River dams (see AMERICAN SHAD AND HICKORY SHAD chapter, this volume).

Odom *et al.*¹²⁵ recently surveyed the use of Virginia tributaries to the Potomac River by anadromous fishes. The study was sponsored by Virginia's Department of Transportation and was designed to assess highway crossings as impediments to fish spawning migrations. They surveyed 148 tributaries in the lower Potomac River downstream of Great Falls and upstream of Popes Creek. Of these tributaries, 40 were confirmed as spawning streams, 83 were deemed probable spawning streams, and 25 appeared to be unsuitable for alosid spawning runs. Barriers to upstream movements were documented on 138 tributaries as follows: stream morphology impediments on 116 streams; roadway crossing barriers on 5 streams; and dams, drop structures or pipeline crossings on 17 streams. Only 10 streams were open their entire length. Beaver dams were not documented in this survey because the authors did not consider them to be permanent blockages to fish passage.

Similar surveys of potential usage of tributaries by anadromous fishes were conducted in the lower and middle James River.^{124,126} In the lower James River (downstream from Richmond), river herring spawning runs were confirmed in 54 tributaries upstream of river mile 40, and 38 tributaries were classified as probable spawning streams. Seven roadway crossings were considered to be impediments to spawning runs. Although the middle and upper James River currently is blocked to spawning runs at Richmond by five dams,² it was concluded that 463 tributaries in the middle James River drainage could be accessible to spawning alosids if they were able to bypass the series of dams at Richmond.¹²⁶ A total of 222 roadway crossings were identified on the 463 tributaries, but only seven were deemed impassable to spawning migrants and seven more were classified as questionably passable. Several projects either have been completed or are in the planning stages for the construction of fish passage facilities at dams on the Rappahannock, James, Chickahominy and Appomattox rivers in Virginia (see AMERICAN SHAD AND HICKORY SHAD chapter, this volume).

Impediments to spawning migrations also are viewed as a major factor which contributed to the decline of alewife populations in North Carolina.¹⁴⁵

Erosion

We could find little evidence that would directly implicate erosion as a factor which contributed to the general

decline of alewife populations in the Chesapeake Bay. Severe floods, intensive agriculture, urban and commercial development, stream channelization and roadway construction in the watersheds of Bay tributaries can accelerate the erosion of surface soils during stormwater runoff and increase levels of suspended solids and siltation rates in water courses. Periodic floods are normal occurrences in alewife spawning and nursery areas that should not affect stock abundance over the long run. However, the turbid water conditions and high flows associated with the severe flooding caused by tropical storm Agnes in June 1972 probably contributed to the decimation of the 1972 year class of alewife in Maryland¹⁴⁰ and in Virginia¹ and altered substrate and depth in many spawning areas.

Fishing Pressure

The recent period of dramatic decline in Chesapeake Bay landings of river herrings overlaps with the years 1967-1974 when foreign fishing fleets heavily exploited herring stocks off the coasts of Delaware, Maryland, Virginia and North Carolina.^{52,158} During these years, the total annual catch of foreign vessels from Bulgaria, East Germany, Poland, Romania, Spain and the USSR averaged 16.2×10^6 kg.¹⁴⁰ In the peak year, 1969, total reported landings of river herring in the foreign fishery were 33.6×10^6 kg. Foreign fleets harvested primarily fish that were less than 190 mm long and mostly immature.¹⁶⁶ This level of fishing pressure on sub-adult river herrings probably was a major factor which contributed to the decline of alewife populations in the Chesapeake Bay and in other southeast Atlantic river systems.^{1,58,166}

Since 1977, the foreign fishery for river herrings within the U.S. Fishery Conservative Zone has been managed; as a result, reported landings have declined.¹⁴⁰ The annual allocation of river herring landings to the foreign fishery between 1977 and 1980 was 0.5×10^6 kg. Since 1981, the total annual allocation has been limited to 100 metric tons (0.1×10^6 kg), less than 2% of the total U.S. river herring harvests in a typical year. However, because the foreign trawl fishery and the joint-venture fishery for Atlantic mackerel takes mostly immature river herrings as a bycatch, the potential for overharvesting effects on the stocks still exists. Even though foreign fishing pressure on river herring stocks in offshore waters has been reduced, alewife populations in Chesapeake Bay have not recovered. Thus, the continuing fishing pressure from the offshore foreign and joint-venture fleets, albeit reduced, coupled with ongoing commercial and sport fishery harvests in the Bay and on the spawning grounds, may constitute a significant increment of mortality on immature and adult alewife that the populations are currently ill-equipped to bear.

BLUEBACK HERRING

Contaminants

Relatively little information exists on the acute and chronic effects of contaminants on various life history stages of the blueback herring.

Toxicity data were located only for chlorine. One study examined the deleterious effects of total residual chlorine (TRC) on blueback herring eggs.¹¹⁰ They reported an 80 h LC₅₀ of 0.33 mgL⁻¹ TRC for blueback herring eggs incubated at 20.9 in 1 ppt salinity.

Two studies examined the effects of TRC on blueback herring larvae. Morgan and Prince¹¹⁰ compared the effects of TRC on 24 h and 48 h old larvae exposed for 24 and 48 h at 20.9°C in 1 ppt salinity. No significant differences in LC₅₀ were observed between age groups or exposure period. For 24 h old larvae exposed for 48 and 54 h, LC₅₀ ranged from 0.24-0.28 mgL⁻¹ TRC; LC₅₀ for 48 h old larvae was between 0.25-0.32 mgL⁻¹. Concentrations of TRC \geq 0.30 mgL⁻¹ increased the percentage of abnormally developed larvae.¹¹¹ The lengths of larvae at hatch were reduced 2.5-5.5% as concentrations of TRC increased during egg development. A single study examined TRC interactions with juvenile blueback herring. Fish held in fresh water avoided 0.1 mgL⁻¹ TRC at 17.5°C.¹³²

Nutrients

See the discussion of nutrients in the **ALEWIFE** section.

Parasites and Diseases

Little is known about the parasites or diseases of blueback herring.¹⁵¹ Sumner *et al.*¹⁶⁸ listed the acanthocephalan *Echinorhynchus acus* as a parasite of blueback herring in the Woods Hole, Massachusetts, region. *Ergasilus chlupeidarum* is a gill parasite in southeastern U.S. waters.⁶⁵ Blueback herring in the St. Johns River, Florida, were parasitized externally by *Lernaea* spp.¹⁸⁴ We could find no information which would implicate parasites or diseases as factors which contributed to the general decline of blueback herring populations in Chesapeake Bay or are preventing stock recovery.

Impediments to Spawning Migrations

See the discussion of impediments to spawning migrations in the **ALEWIFE** section.

Erosion

See the discussion of erosion in the **ALEWIFE** section.

Fishing Pressure

See the discussion of fishing pressure in the **ALEWIFE** section.

SUMMARY AND RECOMMENDATIONS

ALEWIFE

The alewife is a relatively small anadromous clupeid that is distributed along the Atlantic seaboard of North America from northeastern Newfoundland to South Carolina. Alewife are most abundant in the northeast and mid-Atlantic states. In the mid-Atlantic region, alewife occur in New Jersey, Delaware and in virtually all tributaries to the Chesapeake Bay. Landlocked populations occur in many parts of eastern North America, including the Great Lakes and the Finger Lakes in New York.

Schools of adult alewife migrate from nearshore coastal waters to their natal freshwater streams in the spring to spawn. In Chesapeake Bay, spawning typically begins in early to mid-March and extends through April. Alewife tend to favor slow-moving sections of streams above tidal influences for spawning sites.

The juveniles remain in the natal rivers during their first summer and then migrate downstream during the fall as water temperatures decrease. Many juveniles emigrate to the sea, but some may overwinter in deep estuarine waters. The adults return to freshwater for spawning primarily at ages IV and V. The percentage of repeat spawners in Chesapeake Bay varies from year to year and can range from 30 to over 70%.

Alewife and blueback herring are harvested together, generally not distinguished in the records, and reported as alewife or river herrings. Commercial landings of river herrings in the Chesapeake Bay declined dramatically during the 1970's. Recent landings are the lowest ever recorded. Trends in juvenile blueback herring annual abundance indices are also down in Maryland and Virginia.

The decline in alewife abundance during the 1970's was probably caused by an unfortunate mix of several factors that overlapped in time. These factors include at least the following: gradual loss of spawning habitat quantity and quality, over-exploitation of subadults and adults in the offshore foreign fishery between 1967 and 1977, and decimation of the 1972 year class and alteration of many spawning areas by tropical storm Agnes. Residual effects of this major hurricane probably still are being felt almost 20 years later. Efforts to construct fish passage facilities around or over large man-made impediments to spawning migrations and to remove other obstacles (natural and man-made) are accelerating. The answers to key questions about why Baywide populations of alewife haven't recovered seem to lie in the areas of fishing pressure (commercial and recreational) on prespawning and spawning adults in the ocean, the mainstem-Bay and tributaries, spawning habitat quality and quantity, and what can be done to regulate and optimize these factors.

Given the currently low stock levels for alewife in Chesapeake Bay, a moratorium on all fishing inside Chesapeake Bay and strict enforcement of by-catch quotas in the offshore mackerel fishery seem warranted until the stocks show clear signs of recovery. Acidic deposition may be an important threat to water quality in many alewife spawning areas. Studies designed to evaluate mitigation of habitat acidification in the spawning and early nursery areas should continue. Efforts to construct fish passage facilities around or over large man-made impediments to spawning migrations and to remove other obstacles (natural and man-made) should continue to accelerate.

The critical life history stages of alewife are the egg, prolarva, post-larva and early juvenile. The critical life history period in Chesapeake Bay is March through July. A matrix of habitat requirements for the critical life stages is presented in Table 1.

BLUEBACK HERRING

The blueback herring is a relatively small anadromous, clupeid that is distributed along the Atlantic seaboard of North America from Cape Breton, Nova Scotia, to northern Florida. Blueback herring are most numerous in warmer regions from Chesapeake Bay south. In the mid-Atlantic region, blueback herring occur in virtually all tributaries to the Chesapeake Bay, Delaware River and adjacent offshore waters.

Schools of adult blueback herring migrate from coastal waters to fresh or brackish areas in the spring to spawn. In the Chesapeake Bay, the primary spawning runs begin in early April in lower Bay tributaries and in late April in upper Bay tributaries. Blueback herring spawn in freshwater and brackish habitats, often near tidewater, but also far upstream in small tributaries.

The juveniles remain in the natal rivers during their first summer and then migrate seaward in the fall in large numbers when water temperatures decrease to about 15°C. The adults first return to freshwater for spawning at primarily ages IV and V. In general, repeat spawners comprise 30-40% of the spawning runs in the Chesapeake Bay system.

Blueback herring and alewife are harvested together, generally not distinguished in the records, and reported as alewife or river herrings. Reported commercial landings of river herrings in Chesapeake Bay declined dramatically

during the 1970's. Recent landings are the lowest ever recorded. Trends in juvenile blueback herring annual abundance indices are also down in Maryland and Virginia.

The decline in blueback herring abundance during the 1970's probably was caused by an unfortunate mix of several factors that overlapped in time. These factors include at least the following: gradual loss of spawning habitat quantity and quality, overexploitation of subadults and adults in the offshore foreign fishery between 1967 and 1977, and decimation of the 1972 year class and alteration of many spawning areas by tropical storm Agnes. Residual effects of this major hurricane are probably still being felt, almost 20 years later. The answers to key questions about why Baywide populations of blueback herring haven't recovered seem to lie in the areas of fishing pressure (commercial and recreational) on pre-spawning and spawning adults in the ocean, the mainstem-Bay and tributaries, spawning habitat quality and quantity, and what can be done to regulate and optimize these factors.

Given the currently low stock levels for blueback herring in Chesapeake Bay, a moratorium on all fishing inside Chesapeake Bay and strict enforcement of by-catch quotas in the offshore mackerel fishery seem warranted until the stocks show clear signs of recovery. Acidic deposition may be an important threat to water quality in many blueback herring spawning areas. Studies designed to evaluate the mitigation of habitat acidification in the spawning and early nursery areas should continue. Efforts to construct fish passage facilities around or over large man-made impediments to spawning migrations and to remove other obstacles (natural and man-made) should continue to accelerate.

The critical life history stages of blueback herring are the egg, prolarva, post-larva and early juvenile. The critical life history period in Chesapeake Bay is April through July. A matrix of habitat requirements for the critical life stages is presented in Table 2.

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Table 1. Habitat requirements for the critical early life history stages of alewife, *Alosa pseudoharengus*

Life Stage	Zone	Temperature °C	Salinity ‰	Dissolved Oxygen mgL ⁻¹	pH	Hardness mgL ⁻¹ CaCO ₃	Alkalinity mgL ⁻¹ CaCO ₃	Suspended Solids mgL ⁻¹	Current Velocity cm s ⁻¹
egg	Substrate and water column	11-28 (suitable) 16-21 (optimum)	NIF ^a (suitable) 0-2 (optimum)	> 5.0 (suitable) NIF (optimum)	5.0-8.5 (suitable) NIF (optimum)	NIF	NIF	< 1000 (suitable) NIF (optimum)	NIF
prolarva	water column	8-31 (suitable) 15-24 (optimum)	NIF (suitable) 0-3 (optimum)	> 5.0 (suitable) NIF (optimum)	5.5-8.5 (suitable) NIF (optimum)	NIF	NIF	NIF	NIF
postlarva	water column	14-28 (suitable) 20-26 (optimum)	NIF (suitable) 0-5 (optimum)	> 5.0 (suitable) NIF (optimum)	NIF	NIF	NIF	NIF	NIF
early juvenile	water column and near substrate	10-28 (suitable) 17-24 (preferred)	NIF (suitable) 0-5 (optimum)	> 3.6 (suitable) NIF (optimum)	NIF	NIF	NIF	NIF	NIF

^a NIF means no information found.Table 2. Habitat requirements for the critical early life history stages of blueback herring, *Alosa aestivalis*

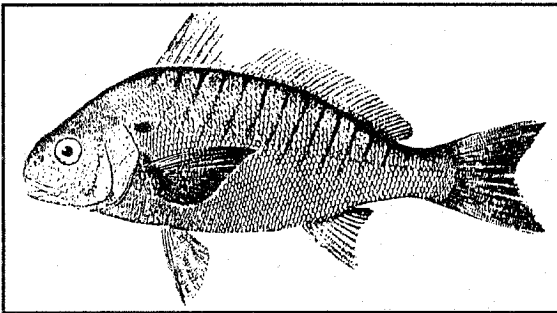
Life Stage	Zone	Temperature °C	Salinity ‰	Dissolved Oxygen mgL ⁻¹	pH	Hardness mgL ⁻¹ CaCO ₃	Alkalinity mgL ⁻¹ CaCO ₃	Suspended Solids mgL ⁻¹	Current Velocity cm s ⁻¹
egg	Substrate and water column	14-26 (suitable) 20-24 (optimum)	0-22 (suitable) 0-2 (optimum)	NIF (suitable) NIF (optimum)	5.7-8.5 (suitable) 6.0-8.0 (optimum)	NIF	NIF	< 1000 (suitable) NIF (optimum)	NIF
prolarva	water column	14-26 (suitable) NIF ^a (optimum)	0-22 (suitable) NIF (optimum)	> 5.0 (suitable) NIF (optimum)	6.2-8.5 (suitable) 6.5-8.0 (optimum)	NIF	NIF	< 500 (suitable) NIF (optimum)	NIF
postlarva	water column	14-28 (suitable) NIF (optimum)	0-22 (suitable) NIF (optimum)	> 5.0 (suitable) NIF (optimum)	NIF	NIF	NIF	NIF	NIF
early juvenile	water column and near substrate	10-30 (suitable) 20-28 (preferred)	0-28 (suitable) 0-5 (optimum)	> 4.0 (suitable) NIF (optimum)	NIF	NIF	NIF	NIF	NIF

^a NIF means no information found.

SPOT

Leiostomus xanthurus

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Spot is and has been one of the most abundant demersal fish species in Chesapeake Bay. Although it doesn't support a major fishery in the Bay, spot is a key species in the trophic dynamics of the Chesapeake as a primary regulator of segments of benthic invertebrate communities and as a prey species.

Environmental degradation has been well-documented in the Chesapeake Bay. Declines in stocks of several species have been related to increased sedimentation, introduction of toxic materials, and nutrient enrichment. Yet, under

these conditions, spot remain quite abundant and provide continuity in the detritus-based food chain of the Chesapeake.

Although spot is an extremely abundant and wide-ranging species, little is known of factors contributing to its stock-recruitment dynamics. Given its ecological importance, more effort should be made to understand what contributes to spot's success and what may be done to assure its continued high level of abundance.

INTRODUCTION

Spot is the most abundant of the croaker family (Sciaenidae) in Chesapeake Bay. Although a relatively small fish, spot supports a commercial fishery, particularly in the lower Bay. Readily caught on hook and line, spot is the species most frequently caught recreationally in many areas of the Chesapeake during the summer and early fall.

Although the dollar value of the spot fishery in the Bay pales when compared to other species such as striped bass, blue crabs, and the eastern oyster, the importance of spot to the economy and ecology of the Chesapeake Bay is quite significant. Spot enhances the viability of Bay fisheries generally as it provides a readily available alternative to fishermen unsuccessful in the pursuit of more desirable species. More importantly, spot is one of the major regulators of benthic invertebrate communities in the Chesapeake, an important forage species, and quite tolerant of poor water quality conditions.

Spot abundance in the Bay appears to have increased in recent years and is currently at a fairly high level. However, as spot are relatively short-lived and their year class success appears to be largely controlled by environmental conditions which occur outside the Bay, few remedial measures are available to resource managers for enhancing or maintaining spot populations. Perhaps the most important of these measures would be increasing summer dissolved oxygen. Although spot are fairly tolerant of low oxygen, hypoxia may have severe effects on spot food resources.

BACKGROUND

Nomenclature, Taxonomy, and General Range

Spot, is one of 13 species of sciaenids reported from the Chesapeake Bay area.⁶⁰ Although spot is the accepted common name, this species is also known by the following common names: Norfolk spot, Lafayette, spot croaker,

jimmy, post croaker, chub, goody, Cape May goody, silver gudgeon, chopla blanca, roach, and oldwife.^{22,42}

Spot range from Massachusetts Bay south along the Atlantic Ocean to Florida and into the Gulf of Mexico as far south as the Bay of Campeche.⁶⁰ There is one report of spot occurring in the Gulf of Maine,⁸ and another from Martinique.²² This species is found in a variety of habitats, from marine to estuarine to brackish, and may be found in depths of less than one meter to depths in excess of 130 m.⁶⁰ In Chesapeake Bay, spot have been collected from all its tributaries and in the mainstem from Capes Henry and Charles to the Elk River.^{17,25,102,105} They occur primarily in brackish to high salinity waters, but also have been found in freshwater areas. They have been taken from all depth zones and over most bottom types.^{53,60,73}

Morphology

Adults

Mature spot are readily discernible from other fish species by the combination of a relatively deep, short, compressed body, a short head with a small, inferior mouth, and a large, black shoulder spot.⁶⁰ Other distinguishing characteristics are an absence of teeth from the lower jaw, a long pectoral fin, extending beyond the tip of the pelvic fin, and a strongly notched, but continuous dorsal fin. Meristic counts for all stages may be found in Johnson.⁶⁰

Juveniles

At 50 mm standard length (SL), spot have virtually all of the characteristics, body shape, meristics, and pigmentation of adult spot. Smaller juveniles, 20–49 mm SL, have a full complement of dorsal spines and rays; they have various pigmentation patterns and may be distinguished from other juvenile sciaenids by a concave caudal fin and the presence of relatively small opercular spines, or else are indistinguishable.

Larvae and eggs

Spot larvae have been described in some detail.^{42,43,60} A description of spot eggs has been reported from a laboratory study.⁹⁵

Distribution

The general distribution of spot in Chesapeake Bay was described above.²⁵ In this section, areas of concentration are discussed.

Adults

Mature spot (>140 mm SL) are found in Chesapeake Bay from April or May through late fall⁶⁰ (Map Appendix); decreasing temperatures apparently trigger seaward migration.⁸⁷ Adult spot distribution in the Bay is not well documented, but the majority of larger spot are taken in Virginia waters and in Tangier Sound. Mature spot also are found during the summer as far north as the Elk River.¹⁰⁵

Recreational fishing for spot appears to be concentrated in river mouths and passages to embayments.

Juveniles

The distribution of juvenile spot (20–140 mm SL) has been well documented and is featured in the Map Appendix. Immature spot, with the exception of occasional overwintering individuals, initially are found in the Bay during April or May, concentrating in Virginia waters and Maryland's lower Bay south of the Patuxent River including Tangier Sound. As the summer progresses, young spot move further up the mainstem of the Bay and into its tributaries. By July, juvenile spot are found from the Elk River south to Capes Henry and Charles and in most Bay tributaries. During the fall, juvenile spot distribution is nearly as extensive as during the summer, but a seaward movement is evident. During most winters, immature spot are absent from the Bay, but during moderate winters some juvenile spot are known to overwinter in deep trenches of the Bay's mainstem.^{17,35,105}

Larvae

Spot eggs hatch in relatively deep coastal waters during the late fall and winter. By the time larval spot reach inshore areas, they are nearing the juvenile stage. Some spot larvae have been collected in the southern portion of Chesapeake Bay,⁹² but those that do reach the Bay as larvae rapidly enter the juvenile stage.

Eggs

Spot eggs have not yet been collected (or recognized) from field studies; they would not be expected to be found anywhere in Chesapeake Bay.

Population Status and Trends

There are few reliable long term data on the abundance of spot in Chesapeake Bay. But several sources pieced together indicate a sharp increase in spot abundance during the early to mid-1970's compared to the preceding 15–20 years.^{49,53,56,102,142,143} Although there were indications of a decline in the mid 1980's, spot continue to be relatively abundant and one of the dominant Chesapeake Bay demersal fish species.^{17,105} Commercial catch records can be misleading because changes in gear, tax laws, and other factors mean that effort does not always reflect availability. But catch records do offer a gross indication of long-term fluctuations in the abundance of spot. Since 1929, spot commercial landings in the Bay have averaged about 2.4 million pounds per year. Periods of high spot abundance occurred during the mid-1940's until 1960, and during the late 1960's, continuing sporadically through the late 1970's (Table 1). Recent landings (1987–89) have been near or above the overall average.

Because spot are short-lived, oceanic spawners, year-class strength is variable and difficult to predict. There is little evidence of stock-recruitment dependence in spot

populations,^{101,122} although there has been limited predictive success with a 2-year lagged stock parent-progeny model describing recruitment in North Carolina.⁶⁷ Long and short term climatological conditions may be most responsible for fluctuations of spot populations. High mortality has been associated with certain temperature ranges, occurrence of freshets, wind conditions during spawning, and changes in oceanic conditions.^{43,61,74,83,139,140}

Commercial and Recreational Importance

Spot has never been a particularly valuable commercial species in the Chesapeake region. Most are landed as bycatch, although there is a pound net fishery for spot in the lower Bay. Commercial landings peaked during 1949 at just over 8 million pounds (Table 1), but even this record catch generated only about \$500,000. Although on occasion spot commercial landings have been valued in excess of \$1 million (most recently in 1989), the dollar value of the spot commercial fishery ranks well below that of other fisheries such as striped bass, Atlantic menhaden, blue crabs, and the eastern oyster.

Since records have been kept, recreational landings of spot have far exceeded commercial catches (Table 1), although in many areas spot is a marginal recreational species. In Maryland, spot are not often sought, but are caught when fishermen are seeking other species.¹⁴¹ In Virginia, larger spot are more abundant than in the Maryland portion of the Bay and are often a recreationally targeted species.

LIFE HISTORY

Spawning

Spot have a rather lengthy spawning period, from late September through March, with peak activity in the mid-Atlantic region reportedly occurring during December and January.^{6,20} Spawning occurs in moderately deep areas along the western Atlantic continental shelf from North Carolina to northern Florida, although this range may extend northward to Delaware, Maryland, and Virginia during certain years.^{29,97,113} Fertilization is external and reportedly takes place at night primarily in surface waters.⁴¹

Development

Eggs

Ova maturation in spot has not been described, although it is known that an individual female's ovaries may contain several developmental stages of eggs. Fecundity has been estimated to range from about 70,000 to 130,000 eggs for 200 mm (SL) spot.^{22,99}

Fertilized spot eggs are buoyant and have been described as pelagic, but have not as yet been collected (or recognized) from field studies. Accordingly, specific locations

of spot spawning activity are not known, nor is the drift pattern of spot eggs. Embryonic development is temperature dependent and ranges from 22 hours at 27°C to 96 hours at 15°C with upper and lower lethal hatching temperatures of 28°C and 14°C.⁴⁰ Embryonic phase development has been described in lengthy detail elsewhere.⁹⁵

Larvae, 1.5-20.0 mm SL

Spot hatch at 1.5-1.7 mm in relatively deep, warm (19.0°C minimum) waters during the late fall and winter. Larvae migrate or are transported inshore and reach North Carolina estuaries about 2-4 months after hatching at about 13 mm SL.^{68,136} In Chesapeake Bay, larval spot 15-22 mm fork length (FL) have been collected as early as April in the southern portion of the Bay.⁸⁶

Larval spot grow rapidly in the warm offshore waters (approximately 7% per day) coincident with the winter plankton peak, but growth slows as they move to cooler inshore and estuarine areas.^{129,136} This movement into colder water may be a particularly critical point in spot year class success as there are indications of larval spot thermal stress at temperatures of 10°C or less.⁵⁸

Larval spot growth has been described from day 11 through day 98 post-hatch¹³⁶ with growth rate estimates ranging from 0.1-0.31 mm d⁻¹.^{99,114} depending on temperature and salinity. Larval spot mortality rates have not been reported, although starvation, temperature, and predation have been suggested as primary causes of mortality.^{58,94,140}

Juveniles, 20-140 mm SL

The range given here for the juvenile stage is based on minimum sizes at which a full complement of spines and rays are present (20 mm) and at which sexual maturity is reached (140 mm).^{22,60,127}

Because of the protracted spawning period of spot, and subsequent multiple juvenile cohorts, the growth rate of zero year class fish is difficult to estimate. In addition, because juvenile spot occur in a variety of habitats and under a wide range of environmental conditions, spot growth rates may differ substantially within a region.⁸⁶ In general, spot reach a length of about 112 mm SL by the end of their first year,^{17,81,82,123} with a range of about 60-150 mm SL.^{16,99} By the end of their second year, spot average about 190 mm SL. Juvenile spot also appear to have a relatively short growing season: from April or May through September or October.^{54,99,105,140}

Juvenile instantaneous coefficients of mortality have been estimated to be between 0.02 and 0.06.^{21,99,140} These estimates predict annual mortality of juvenile spot as high as 90%, caused principally by predation and low water temperatures. Massive winter kills have been reported in Chesapeake Bay and elsewhere.^{12,23,143}

Adults, ≥ 141 mm SL

Spot reach sexual maturity near the end of their second year or early in their third year.^{22,81,82} Size at maturity appears to be quite variable, with minimum lengths reported in the range of 135-179 mm SL.^{92,42}

As with juvenile spot, adult growth is difficult to estimate. Between the second and third years, spot growth approaches a 40 mm SL increment, and from the third to fourth years about 25 mm.^{4,60,112} Spot older than age class III apparently rarely are caught in Chesapeake Bay.⁹⁹ Adult spot annual mortality has been estimated to be about 80% of the population.⁸⁶

ECOLOGICAL ROLE

Throughout most of their range, including Chesapeake Bay, spot repeatedly have been referred to as among the most abundant demersal fish species during the late spring and through the late fall.^{17,55,56,65,88,127} Their high densities, along with their high rate of growth, suggest that spot have a large impact on their prey populations and are an important food source for other species.

Food Habits*Larvae*

Larval spot are planktivorous and feed primarily during daylight hours.^{33,93} Because movement of both larval spot and their prey is controlled largely by currents, the coincidence of larval and plankton patches appears to be critical in the growth and survival of spot larvae.^{34,64}

Juveniles and Adults

Spot are obligate bottom feeders, well-adapted morphologically to scoop and strain organisms from substrates. These adaptations - a short snout, inferior mouth, a protrusible premaxilla, gill rakers structured and configured efficiently for straining small organisms, and a large number of nasal laminae - indicate an animal that feeds indiscriminately on benthic infauna using odor to locate patches of prey organisms.^{16,52,104} Spot appear to be non-periodic feeders, with evidence that feeding is either continuous or that feeding episodes occur frequently.^{52,93}

Throughout their ranges spot feed primarily on copepods (as small juveniles), polychaetes, and small molluscs.^{1,24,26,42,44,45,65,119} They also show a preference for feeding over muddy sediments, a bottom type for which spot are particularly well adapted.^{9,16,104,116} Several Chesapeake Bay studies of spot food habits are summarized in Table 2. These studies indicate the importance of small benthic infaunal invertebrates in the diet of spot and the low percentage of empty stomachs.

Predation

Predator-prey interactions appear to be extremely significant to juvenile spot. In Chesapeake Bay there is a

general, often sharp, decline in benthic macroinvertebrate stocks during mid-summer.^{46,48} This decline occurs shortly before the end of the growth period of juvenile spot, beginning during the period of greatest juvenile spot abundance.

Little is known about natural predators of adult spot. Striped bass, the silky shark, weakfish, and bluefish have been reported as predators of large spot.^{22,51,52} It has been speculated that adult mortality is quite high after the spawning run.^{86,90}

A number of studies have concluded that fish can have significant effects on the density of prey populations,^{3,30,63,91,146} and in particular that spot predation may control the density of a number of benthic invertebrate species.^{27,54,132} During several caging experiments, spot were found to have significant impact on densities of epibenthic copepods²⁷ and on a number of species of polychaetes and small bivalves.^{132,133} Studies of benthic invertebrate densities, predator exclusion experiments in the mid-Chesapeake Bay area,^{46,48} and concurrent studies of spot abundance,¹⁴² growth, and food habits,⁵² indicated that 100% of the May-September decline in polychaete densities and about 68% of the decline in small bivalve densities were attributable to spot predation. Spot have been characterized as the major regulators of a large component of the mid-Chesapeake Bay benthic invertebrate community.⁵⁴

In addition to regulating the abundance of numerous prey species, spot may play a large role in determining the structure and microdistribution of benthic communities and in the resuspension of surface sediment materials. Several studies^{27,84,133} have shown benthic invertebrate community structure (species composition and dominance) to be greatly influenced by spot predation.

Where spot are present in large numbers, the benthic community may have few non-burrowing species, or those non-burrowing species present are minor components of the benthic community.^{49,132,133} Spot predation affects the distribution of organisms within the substrate. Burrowing invertebrates have been shown to migrate vertically to avoid the shallower sediment layers where spot feed.²⁷ One study⁹ estimated that the entire upper 2 mm of sediment within spot feeding areas would be turned over once every 120 days. It is not known how this bioturbation affects the movement of materials in sediments, aeration of sediments, or the feeding behavior of other benthic predators, but given the great abundance of spot throughout much of their range, their impact must be substantial.

The importance of spot as prey for other species has not been well documented. Although a number of studies have listed spot as prey of other fish species, their ener-

getic contribution to these predators is not known. Spot larvae have been reported in the diets of silversides and the striped killfish¹⁴⁰ and as probable prey of chaetognaths.¹⁹ Spot juveniles have been reported to be eaten by numerous fish species, including weakfish, bluefish, striped bass, white perch, Atlantic croaker, silver perch, summer flounder, American eel, brown bullhead, white and channel catfish, and oyster toadfish.^{7,13,51,52,71,77,120,124} It has been suggested that predation may be the most important factor in limiting juvenile spot production, particularly in the more saline areas.²¹ However, the importance of spot as prey has not been documented as yet, nor has the role of predators in regulating spot populations.

HABITAT REQUIREMENTS

Spot is an extremely adaptable species, as indicated by its extensive geographical range and the variety of habitats in which it is found. Thus, it is not surprising that spot are tolerant of wide ranges of environmental factors, and show little preference for specific habitats with the exception of substrate. There are, however, some factors in Chesapeake Bay which may affect spot year-class success.

Water Quality

Preferred and overall ranges, and upper and lower critical values of temperature, salinity, dissolved oxygen, and suspended sediments for post larval and juvenile spot in the Chesapeake Bay are given in Table 3.

Temperature

Spot rarely encounter temperatures in Chesapeake Bay near or above their critical thermal limit (31°C). However, temperatures near or below their lower thermal limit (4-5°C) are not uncommon in the Bay during the winter months. Juvenile spot, overwintering because of a mild early winter, are susceptible to sudden decreases in water temperature as evidenced by reports of massive winter fish kills in the Bay.⁹⁹ Since those spot that overwinter appear to be a second, smaller cohort of young of the year, year class success could be affected by winter conditions.^{23,56,99,105} Outside the Bay, temperature affects larval survival, and within the Bay it may affect juvenile growth and mortality through its impact on prey species.^{43,96,99,144}

Salinity and freshwater runoff

Spot are tolerant of a wide range of salinities, having been found in fresh water and in hypersaline (60 ppt) areas (Table 3). It has been suggested that fluctuations in salinity rather than actual salt concentrations control the local distribution of spot.⁹² However, spot appear to be well-adapted to tolerate extreme salinity changes, so environmental factors associated with salinity fluctuations resulting from freshwater runoff, such as higher turbidity, herbicides, and pesticides, may have more influence on spot distribution than actual changes in salinity.⁸⁰ These adverse conditions could limit the range of juvenile spot

in the Bay's tributaries and in the upper Bay, and could affect spot year class success by reducing available prey resources, thus increasing predation on spot.^{21,140}

Dissolved oxygen

Spot appear to be fairly tolerant of low dissolved oxygen (DO); they have been found on occasion in areas of less than 2.0 mgL⁻¹.^{15,105,126} In general, however, they are most abundant where DO exceeds 4.0 mgL⁻¹.^{16,73,105} Severe hypoxia, which occurs regularly in deeper areas of the Bay, may somewhat restrict spot distribution, but spot feed primarily on organisms found in depths of less than 10 m.^{47,48} Most of the prey species of spot are not tolerant of low DO (< 2.0 mgL⁻¹)¹³¹, therefore spot abundance may be affected by low DO in their feeding grounds.

Suspended and deposited sediments

Spot are extremely tolerant of high levels of suspended and deposited sediments^{115,128} and, in fact, a positive relationship between spot abundance and dredging activity has been reported.¹²² This may be related to feeding behavior as spot have shown a preference for muddy sediments and are well-adapted for feeding in such habitats.^{16,104,116}

Perhaps it is no coincidence that the relatively recent increase in spot abundance in the Chesapeake Bay occurred shortly after tropical storm Agnes tore through the Bay in June 1972. Agnes discharged massive amounts of suspended sediments from flooded rivers into the Bay.¹¹⁰ During a 10-day period, the major feeder of fresh water into the Chesapeake, the Susquehanna River, discharged more sediment into the Bay than it normally does in 30-60 years.¹¹⁰ Discharge from the river systems also caused extended periods of lower than normal salinities in much of the Bay, and the combination of fresh water and organic loading produced zones of low DO.^{2,10} These conditions had a profound effect on benthic invertebrate communities in the Bay, particularly in polyhaline areas.¹⁰ The combination of widespread changes of bottom type and subsequent changes in the benthic invertebrate communities may have been largely responsible for the relatively recent increase in spot abundance in the Bay.

Structural Habitat

Habitat preference and general and preferred ranges of depth and substrate for Chesapeake Bay postlarval and juvenile spot are given in Table 3.

Depth

Although occurring in all depths of the Bay, spot tend to be most concentrated in the 6-10 m zone in the mainstem and in sounds, and in 3-6 m depths in tributaries except during fall months.^{53,54,105} It is probable that spot distribution by depth is related primarily to food sources, as these zones support large benthic invertebrate communities.^{46,47} During moderate winters, juvenile spot seek out

deep trenches or holes where temperatures may remain above their lower lethal thermal limit.

Substrate

Spot appear to prefer mud or mud-sand mixtures of sediments (Table 3). As with depth, prey abundance apparently controls the distribution of spot with respect to substrate. Spot feed most easily and efficiently in soft substrates. They rarely are found over or in submerged structures.

SPECIAL PROBLEMS

Contaminants

The developmental stages of spot are not directly exposed to toxicants in the Bay. However, indirect exposure through water-borne materials, consumption of contaminated prey, or the legacy of adult spot exposed to contaminants in the Bay could affect fecundity or early development of the offspring. Apparently, there have been no studies of these secondary effects.

The toxicities of a variety of inorganic and organic compounds to various life stages of spot (mostly juveniles and adults) have been measured (Table 4). Some insecticides (e.g., dieldrin, endrin, endosulfan, toxaphene) are lethal to juvenile spot at very low concentrations.

Chlorine (total residual; TRC) causes effects in juvenile spot ranging from avoidance ($> 30 \mu\text{g/L}^{-1}$)⁹⁸ to 100% mortality in 96 h ($\geq 160 \mu\text{g/L}^{-1}$).⁵ Apparently, the lethal threshold for juvenile spot in relatively short term exposures to TRC is somewhat greater than $40 \mu\text{g/L}^{-1}$.^{5,77}

Spot have been exposed to contaminated sediments from Baltimore Harbor and the Elizabeth River under controlled conditions.^{37,128} Suspensions of Baltimore Harbor sediments with high concentrations of metals, hexane extracts (non-polar organic contaminants) and polychlorinated biphenyls (PCB) had TLm values for spot at concentrations of 0.06 - $29.12 \mu\text{g/L}^{-1}$, or 60% to 0.1% of the TLm for clean sediments.¹²⁸ Elizabeth River sediments with PAH concentrations of 2500 - 3900 mg kg^{-1} dry weight caused severe sublethal effects and mortality in spot.³⁷ Spot captured in the Elizabeth River had marked reductions in macrophage phagocytosis (a cellular disease defense mechanism), which were reversible after several weeks in clean water.¹³⁸ Exposure to contaminated sediments is of particular concern for spot in Chesapeake Bay, because of their feeding habits and preference for areas with fine-grained sediments. Their benthic prey also can concentrate contaminants from sediment. These considerations suggest spot as an important species for monitoring tissue concentrations of persistent pollutants such as PCB and PAH.

Diseases

No reports concerning diseases of Chesapeake Bay spot could be found in the literature; nor have mass mortalities of spot been attributed to disease. However, both of us have observed tumors in the body cavities of spot on a number of occasions; in addition various morphological deformities, perhaps disease-related, have been reported.⁹⁹

Spot are vulnerable to only one parasite, an acanthocephalan (a wormlike animal), to any significant degree.^{59,70,137} This parasite, which has been reported to infect as much as 75% of the spot population,⁸⁵ apparently does not have any particular effect on its host.⁵⁹ Other common Chesapeake Bay fish parasites such as isopods, copepods, and trematodes have been found only rarely to affect spot.^{22,66,70,125,134}

RECOMMENDATIONS

1. Research should be conducted on spot stock-recruitment dynamics, predator-prey relationships with emphasis on spot as prey, and the development of an annual recruitment index.
2. Spot should be included as one of the many species that could benefit from reduced hypoxia during summer in Chesapeake Bay.
3. Spot over-wintering grounds and the work being done to preserve these areas need to be documented.
4. Finally, the potential of spot commercial and recreational fisheries should be estimated.

CONCLUSIONS

Spot are and have periodically been among the most abundant demersal fish species in Chesapeake Bay. Of all the marine-estuarine fish species, spot has the most extensive Chesapeake Bay distribution. Spot are one of the major regulators of benthic invertebrate communities, particularly in the muddy, shallower ($< 10 \text{ m}$) zones of Chesapeake Bay. The abundance, extensive distribution, small size, and relatively high rate of growth of spot suggest a species of intrinsic importance in the predator-prey dynamics of Chesapeake Bay. Spot may indeed be a "foundation" species.

Spot are highly tolerant of a wide range of water quality and habitat conditions. This adaptability in combination with "r" selected characteristics - that is, spot are short-lived and have high rates of reproduction and growth - has produced an opportunistic species, one that can take advantage of conditions that result in declines of other fish species. During periods of chronic stress, spot are able to maintain important trophic links in Chesapeake Bay.

Although not as important to the bay economically as striped bass, blue crabs, and oysters, spot do support a small commercial fishery, particularly in the lower Bay. Spot generally are not considered a prized catch, but their great abundance and catchability allow recreational fisherman to fill their coolers when other, more desirable species elude them.

The key question is this: because spot are a critical Bay species, how can we assure their continued abundance? The question presents a dilemma to Chesapeake Bay fishery and resource managers. Fundamental to fishery management is the understanding of stock-recruitment relationships, that is, what factors most influence year

class success. Currently, little is known about spot stock-recruitment dynamics. This lack of knowledge, the species' high degree of tolerance, and the possibility that their most critical life-stage occurs outside the boundaries of Chesapeake Bay, have combined to deflect management attention from spot. Given the ecological importance of spot, however, the species and its fishery need to be better understood.

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Table 1. Chesapeake Bay landings of spot (millions of pounds). * = greater than overall mean of 2.45.

Year	Commercial ¹¹	Year	Commercial	Recreational ¹³⁰
1929	0.85	1958	5.05*	
1930	1.65	1959	3.70*	
1931	0.65	1960	4.20*	
1932	0.80	1961	1.15	
1933	0.55	1962	2.35	
1934	1.70	1963	1.45	
1935	0.30	1964	3.20*	
1936	0.95	1965	1.75	
1937	2.00	1966	1.05	
1938	3.20*	1967	3.15*	
1939	2.50*	1968	1.15	
1940	1.85	1969	1.00	
1941	1.55	1970	6.05*	
1942	0.55	1971	0.55	
1943		1972	2.95*	
1944	0.20	1973	2.35	
1945	0.25	1974	2.15	
1946	4.00*	1975	1.50	
1947	4.45*	1976	1.05	
1948	3.95*	1977	1.65	
1949	8.15*	1978	2.85*	
1950	4.60*	1979	2.40	5.05
1951	4.90*	1980	1.85	8.60
1952	5.95*	1981	1.05	10.50
1953	3.95*	1982	1.00	5.60
1954	4.45*	1983	1.70	10.75
1955	4.00*	1984	0.80	5.55
1956	3.20*	1985	1.55	6.05
1957	3.45*	1986	1.95	7.80
		1987	4.0*	7.75
		1988	2.6*	2.75
		1989		5.50

Table 2. Summary of spot stomach contents from selected Chesapeake Bay studies. Major prey items are listed.

Location	Calvert Cliffs, Maryland ⁵⁶	Patuxent River, Maryland ⁵⁵	Calvert Cliffs, Maryland ⁵²	Eastern Bay, Maryland ¹³
Spot size range	60-230 mm TL	50-220 mm SL	20-154 mm SL	25-135 mm
Empty (%)	5.0	9.7	5.1	
Prey Items	Occurrence %	Weight %	Weight %	Weight ^a %
polychaetes	65	9	83	30-68
molluscs	42	49	10	0-4
mysid/grass shrimp	18	3	1	9-0
detritus	15			8-5
amphipods	9	2	2	3-5
copepods	9	34	2	1-0
isopods	8	0	1	0-0
bryozoans	0	0	0	20-0

^a First value is from vegetated area; 2nd value from non-vegetated area.

Table 3. Upper and lower critical values and general and preferred ranges of temperature, salinity, and dissolved oxygen for postlarval and juvenile spot in Chesapeake Bay. na = not available; nap = not applicable.

	Preferred	Lower limit	Upper limit	Range	Reference
TEMPERATURE (°C)					
	6-20				88
	18				76
	25				75,144
		4-5			43
		5			22
			31		57
			35		45
			38		32
				1.2-37	32,88
SALINITY (ppt)					
	none ^a		na		18,62,105
		< 2			101
				0-60	39,60
DISSOLVED OXYGEN (mgL ⁻¹)					
	> 2.0		nap		105
	> 5.0				84
		0.4 (ml L ⁻¹)			126
		0.7			15
		0.4-1.3			105,84
SUSPENDED OR DEPOSITED SEDIMENTS (g/L ⁻¹)					
	nap	nap	88.0 ^b		115
			50.6 ^c		128
DEPTH (m)					
	0.5-15 ^d	nap		54,60,105,119	
			seasonal ^e		105
				0.5-37	35,54,105
SUBSTRATE					
	mud				22,54,116,122
	mud/sand				105,117,141
				mud-sand ^f	13,54,60,116

^a No strong preference; small juveniles tend to prefer low salinities, whereas larger fish show no preference.

^b 24 h LC₅₀: Patuxent River silt.

^c 24 h TLM: fuller's earth.

^d variable.

^e warm months to about 20 m.

^f most commonly found over mud and over sand; not associated with shell, rubble, or submerged aquatic vegetation.

Table 4. Acute toxicity of selected toxicants to various life stages of spot. Life stage: E = eggs; L = larvae; J = juveniles; A = adults; NR = not reported. Where salinity is not given, tests were conducted in saline water.

Substance	Life stage	Salinity ppt	Temperature °C	Effect	Concentration $\mu\text{g L}^{-1}$	Reference
INORGANIC						
bromate	J	5.1	20.1	10 d LC ₅₀	278600	100
bromine (tot. res.)	J	2.0	29-32.4	no mort. (19 d)	20-81	69
bromine chloride	J	20	19-28	96 h LC ₅₀	220	103
cadmium	L	16-19	15-22	"	31	79
	L	17-20	17-20	stress ^a	≥ 500	29
	A	15	22	48 h LC ₅₀	35000	38
	A	15	22	sublethal	≥ 10000	
chlorine (TRC)	J	20-24	10	incipient LC ₅₀	120	78
	J	20-24	15	incipient LC ₅₀	60	
	NR		14.2-16	24 h TL _m	140	5
				96 h TL _m	90	
				100% mort. (96 h)	≥ 160	
				0% mort. (8 d)	≤ 40	5,78
	33-115 mm	3-8	16-26	avoidance	30-300	97
	J	19-22	15,20	"	50	69
	J	19-22	10	"	180	
	J	2.0	29-32.4	mortality (20 d)	14-62	
	J	20-24	15	gill damage (95 min.)	1570	78
copper	E		17	50% mort. (24 h)	101 ^b	28
	E		17	hatch reduced (4 d)	25.3 ^b	
mercuric chloride	A	20	26	96 h LC ₅₀	36	50
nickel chloride	A	21	26	"	70000	31
potassium dichromate	A	21	26	"	27000	14
ORGANIC						
acephate	A	20	25	96 h LC ₅₀	>100000	31
aldicarb	A	20	25	"	200	
aldrin	J	28	24	48 h LC ₅₀	3.2	
ametryn	J	29	28	"	>1000	
anilazine	J	23	29	"	8.5	
antimycin A	J	28	25	"	0.23	
atrazine	J	29	28	"	>1000	
	NR	12	22	96 h LC ₅₀	8500	135
azinphos-methyl	J	21	21	48 h LC ₅₀	28	31
bensulide	A	21	25	"	320	
bromacil	J	18	13	"	>1000	
carbophenothion	A	20	25	96 h LC ₅₀	500	
	A	24	26	"	>210	
chlordecone	J	26	22	48 h LC ₅₀	130	
chlordecone	A	18	25	96 h LC ₅₀	6.6	
chloropropylate	J	26	14	48 h LC ₅₀	320	
chlorothalonil	J	22	11	"	32	
DDE	J	26	12	"	>100	
DEF	J	26	27	"	240	
	A	20	25	96 h LC ₅₀	150	
	J	20	26	"	130	
demeton	J	27	26	48 h LC ₅₀	320	
diamidfos	J	29	30	"	>1000	
dicamba	J	29	30	"	>1000	
dichlofluanid	J	29	13	"	32	
dichlorvos	J	25	28	"	320	
dieldrin	J	25	12	24 h LC ₅₀	3.2	
in acetone	J			sublethal (4 d)	1.35	89
"	J			none	≤ 0.135	

Substance	Life stage	Salinity ppt	Temperature °C	Effect	Concentration µg L ⁻¹	Reference
dimetilan	J	25	12	48 h LC ₅₀	>1000	31
endothall (Aquathol plus)	J	28	27	"	>1000	
endrin	J	24	12	"	0.3	
	J	23	17	24 h LC ₅₀	0.45	72
	J			sublethal (8 mo.)	< 0.05	
endosulfan in acetone (Thiodan tm)	A	18	25	96 h LC ₅₀	0.09	108
EPN	A	23	24	"	26	31
ethion	J	31	27	48 h LC ₅₀	70	
ethoprop	A	20	25	96 h LC ₅₀	33	
fenac sodium salt	J	23	13	48 h LC ₅₀	>1000	
fenthion	J	23	19	"	1200	
fenuron	J	20	25	"	>1000	
fonofos	J	28	24	"	240	
heptachlor in acetone	J	20	25	100 % mort. (6 d)	2.55	107
65% in acetone	J	20-21	23-26	96 h LC ₅₀	0.85	106
99.8% in acetone	J	20-22	24.5-25.5	"	0.86	
hexachlorocyclo- pentadiene	A	24	25	"	37	31
isobenzan	J	22	13	48 h LC ₅₀	0.32	
kepone in food	J	17.7-18	23-28	sublethal (4 wk)	3.3 µg g ⁻¹	118
	J	20.3-21.8	16-23	sublethal (56 d)	0.3-0.59 µg g ⁻¹	
in acetone	J	18	25	96 h LC ₅₀	6.6	109
leptophos	J	23	22	"	4.1	31
lindane	J	23	15	48 h LC ₅₀	23	
malathion	J	24	19	"	320	
	J	2.5-2.7	23-29	sublethal ^c (182 d)	10	
methidathion	J	25	12	48 h LC ₅₀	32	
methoxychlor	J	26	22	"	23	
methyl parathion	A	12	22	96 h LC ₅₀	59	
mirex	J	27	22	48 h LC ₅₀	>2000	
molinate	J	20	25	"	>1000	
naled	J	20	20	"	240	
neburon	J	20	25	"	320	
nitrapyrin	J	20	16	"	>1000	
parathion	J	22	14	"	18	
Pentron D-90 tm	J	6.8	25	no mort. 96 h	5000	14
phorate	A	18	25	96 h LC ₅₀	3.9	31
phosphamidon	J	29	23	48 h LC ₅₀	>1000	
phoxim	J	29	29	"	2.8	
prometryn	J	29	29	"	>1000	
ronnel	J	24	13	"	320	
silvex propylene glycol butylether ester (Kuron tm)	J	20	16	"	360	
2,4,5-T propylene glycol butylether ester	J	20	16	"	320	
temephos	J	23	23	"	>1000	
terpene polychlorinates	J	27	25	"	3.2	
tetrachlorvinphos	J	25	17	"	>1000	
tetrasul	J	29	16	"	>1000	
thanite	J	22	14	"	32	
toxaphene	J	25	12	"	3.2	
in acetone	J	32-35	18	96 h LC ₅₀	0.92	36
degraded	J				1.10	

^a Critical thermal maximum and resistance to low dissolved oxygen decreased after 96 h pre-exposure to 500 µg L⁻¹ cadmium.

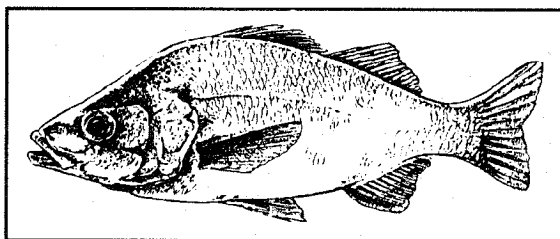
^b Measured as cupric ion activity.

^c No significant differences in growth or mortality. Brain cholinesterase reversibly reduced in experimental groups.

WHITE PERCH

Morone americana

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White perch, a semi-anadromous species and one of the most abundant fish in Chesapeake Bay, spends its entire life in the Bay and its tidal tributaries. White perch migrate to tidal fresh and slightly brackish waters each spring to spawn. After spawning, adults move downstream to more brackish areas; summer movements are local and random. White perch overwinter in the downstream portions of the tributaries and deeper saline waters

throughout the Bay, usually at depths greater than 6-12 meters, in areas with salinities in the 'teens. White perch support commercial and recreational fisheries in Maryland and Virginia. From 1980-1985, Maryland commercial catches ranked from second to fourth both in pounds landed and in dollar value. Recreational catches exceed commercial catches in some years.

White perch concentrate in areas with dissolved oxygen concentrations (DO) of at least 6 mgL⁻¹. Increasing bottom DO in summer months to at least 5 mgL⁻¹ in the oligohaline and mesohaline portions of the Bay will increase suitable habitat for white perch. Growth rates and longevity of white perch stocks within Chesapeake Bay may vary widely. A realistic white perch fishery management plan must be based on stock-specific growth and mortality rates.

INTRODUCTION

White perch is one of the most abundant fish in Chesapeake Bay. The species was second in abundance in the Choptank and Patuxent Rivers and third in the upper Bay in recent intensive surveys.⁷³ Although closely related to striped bass - they are in the same family (Percichthyidae) and the same genus - adult white perch are quite distinct in appearance, behavior, and seasonal distribution. They are smaller than striped bass and lack their distinctive stripes. Adult white perch typically range in size from 165-190 mm (6.5-7.5 inches), although they can reach 300 mm (12 inches) in length. Their weight rarely exceeds 0.5 kg (1.1 lb). Most males mature by two years of age, most females by three years, and few of either sex live beyond nine or ten years. White perch tend to inhabit open waters close to shore, and deeper channel areas where they overwinter, but they also frequent quiet streams well up into the tributaries. They are bottom-oriented fish, and adults are rapacious predators on all forage species.⁴⁰

White perch support important commercial and recreational fisheries in Maryland and Virginia because of several characteristics which are unique among the important anadromous and semi-anadromous species in the Bay. Richkus and Stroup's⁷⁰ comments were limited to Maryland, but could apply equally to Virginia: "White perch are present and available for harvest in Maryland waters during all seasons of the year; they are a very desirable food species; and they are found throughout the Maryland portion of the Bay. Unlike other anadromous species whose population levels can be influenced by exploitation in and environmental degradation of non-Maryland waters, population fluctuations of white perch are a result solely of factors operating within Maryland. Thus stock levels can be responsive to management actions taken solely in Maryland."⁷⁰

Commercial landings of white perch in Maryland exceeded two million pounds in 1966, 1968, 1969, and 1971. From 1980 to 1985 white perch ranked from second to

fourth both in pounds landed and in dollar value among Maryland commercial catches. Recreational catches of white perch exceed commercial landings in some years. Maryland's recreational catch was 1.2 million and 0.75 million pounds in 1979 and 1980, respectively; approximately twice the commercial harvest in 1979 and 70% of the commercial harvest in 1980.⁷⁰

White perch apparently require good water quality; they concentrate in areas with DO of at least 6 mgL⁻¹.⁷³ Increasing eutrophication of the Patuxent River and the resulting increase of hypoxic bottom waters around Broomes Island apparently have made the middle Patuxent unsuitable habitat for white perch (they dominated monthly trawl catches from Broomes Island during 1965-68, but were extremely rare there in 1988-89).⁷³

BACKGROUND

Mansueti's study of the Patuxent River population⁴¹ is the most comprehensive available for estuarine white perch. Other extensive studies have been conducted in the Choptank, Delaware, and Hudson River estuaries.^{13,34,66} The evaluation of Maryland white perch by Richkus and Stroup⁷⁰ serves as the basis of the White Perch Fishery Management Plan currently being prepared by the Maryland Department of Natural Resources (MDNR).

Geographical Range

White perch are endemic in Atlantic coastal waters from Nova Scotia to South Carolina,⁹⁵ and are most abundant between the Hudson River and the Chesapeake Bay.⁸⁰ This euryhaline species inhabits marine, estuarine, and tidal fresh waters, with the largest numbers found in brackish waters.⁴¹ Since the late 1880's stocking, canal building, and other human activities have extended the original range north and west into the waters of Quebec, Lake Ontario, and Lake Erie.^{12,36,79,82} By 1978 white perch populations were found in all coastal states and maritime provinces from South Carolina to Prince Edward Island, and inland from Vermont and Ontario along the Great Lakes to Michigan and into Nebraska.^{29,79}

Migrations and Movements

White perch migrate from lower estuaries to fresh water to spawn, thus they are a semi-anadromous species. Chesapeake Bay white perch spend their entire lives in the Bay, migrating up into the tidal fresh and slightly brackish waters of its tributaries each spring to spawn. Adult white perch overwinter in the downstream portion of tributaries and in deeper saline waters throughout the Bay usually at depths > 6-12 m, in areas with salinities in the 'teens and water temperatures from < 0 to 4°C.^{30,41,55} These distributions are shown in the Map Appendix.

As water temperatures increase in the spring, sexually mature adults begin moving upstream to fresh or slightly

brackish spawning areas. Ripe males generally precede females into the spawning grounds.⁹² Spawning migrations begin by the latter half of March, and by the end of March or the first week of April most ripe adults are on the spawning grounds. After spawning, adults move downstream, primarily to brackish areas in the middle and lower portions of tributaries. However, in the Susquehanna River below Conowingo Dam and on the Susquehanna Flats, adults can be found in fresh water in great abundance all summer (Map Appendix).

Summer movements are local and random, rarely covering more than 12 miles (~19 km).^{27,41,86} White perch generally move inshore to shallows 1.5-3 m deep to forage at night, and offshore to deeper waters (3-6 m) at dawn. Movement to overwintering areas begins as water temperatures decline in October and November.^{30,41,55}

Patuxent River white perch remain in the river throughout their life cycle,⁴¹ migrating from the lower and mid-estuary upstream to tidal fresh waters for spawning in the spring, engaging in local and random movements in summer, and usually migrating downstream toward deeper water in the fall. White perch overwinter in the mid- and lower Patuxent at water depths of 6-30 m.

A recent trawl survey clearly demonstrated the preference of white perch for upriver, low salinity habitats. In the Patuxent River white perch were rarely found below river mile (rm) 18 (km 29) at Long Point until November, when they were concentrated near Battle Creek at rm 14 (km 23). Peak abundances during the winter of 1989 were at Long Point. However, from March through September, peak abundances were upriver, six to ten miles (10.7-16.1 km) above Long Point. The upriver distribution during summer may be due to bottom-water hypoxia in the mid-portion of the Patuxent estuary (see **Special Problems**).

In the Choptank River, white perch were never collected below rm 17 (km 27) during the recent trawl survey. Peak abundance during December and January was from rm 26 (km 42) at Lloyds Landing to rm 42 (km 68) at Denton. By February peak abundances were further downriver at rm 17 and 26, whereas from April through October peak abundances were recorded at rm 17. Likewise, in Chesapeake Bay, white perch occur essentially only in the river-like area above the Bay Bridge⁷³ (Map Appendix).

White perch populations tend to be somewhat segregated by size, with larger white perch at downstream locations within the estuary, and the smallest fish only at upstream locations. Thus, for example, in the Patuxent River medium-sized white perch [100-180 mm total length (TL)] were concentrated between rm 15-25 (km 24-40), whereas large white perch (> 180 mm TL) were concentrated between rm 15-20 (km 24-32). In the Choptank River

medium-sized white perch were concentrated between rm 10 and 30 (km 16-48), whereas the largest white perch were concentrated between rms 5-15 (km 8-24).⁷³

Tagging and morphometric studies suggest that riverine populations of white perch in the Bay are at least partially isolated.^{41,95} Salinity gradients may prevent inter-river migrations of white perch, especially in the lower Bay.⁶⁴

Analysis of mitochondrial DNA (mt DNA) variation from seven tributaries (the James, York, Potomac, Patuxent, Sassafras, Choptank, and Nanticoke Rivers) and the upper Bay (Hart and Miller Island) provided evidence for ten distinct matriarchal clones of white perch in the Bay,⁶⁴ clustered into three major groups: (1) a large aggregation including the Hart and Miller Island areas, along with the Nanticoke, Choptank, Sassafras, and Patuxent Rivers (where a single genotype was evident); (2) the Potomac River; and (3) a lower Bay population including the James and York Rivers.

Abundance and Recruitment

White perch have a propensity for "stunting," which results in populations of high abundance but low growth rates and mean size (density-dependent growth).⁷⁰ Growth rates of juvenile white perch are affected by temperature, food supply, and population density. Growth of juvenile white perch in the Patuxent River was correlated positively with the number of spring days with water temperatures between 10-15°C and the amount of solar radiation, whereas the amount of spring rainfall and the size of the population both were correlated inversely with growth.⁴¹ Density-dependent growth of white perch also has been reported in the Susquehanna River and other areas outside the Bay region.^{20,43,82,90,93}

The only index of abundance of the estuarine white perch population of the upper Chesapeake Bay is the Maryland Juvenile Index (JI) - the average number of young-of-year white perch caught per seine haul (duplicate samples at 22 stations in the Maryland portion of the Bay and its major tributaries in July, August, and September). Juvenile abundance generally has been lower since 1970 with no sustained high production comparable to 1959-1961 and 1969-1970 (Table 1).⁷⁰

Major year classes vary from region to region and year to year, apparently because of variations in the suitability of environmental conditions for reproductive success.⁷⁰ For example, high production occurred around 1960 in the Potomac, Nanticoke, and Choptank Rivers, but not in the upper Bay. In 1969 and 1970 the highest production was in the upper Bay and the Nanticoke River (Table 1). Likewise, dominant year classes in 1964 and 1965 were produced in the James River, but not in the York River.⁸⁵

The JI probably is not an adequate measure of relative year class size in Maryland as a whole. Although the JI averages overall catch from 22 stations spread throughout Maryland waters in the Bay, most Maryland white perch are concentrated in the upper Bay area.⁷⁰ No significant relationship was found between Baywide commercial landings and the JI lagged over a number of years bracketing ages known to be captured in the fishery. However, when the same techniques were applied to the Potomac River mainstem, 87% of the variance in the white perch catch could be explained by the Potomac River JI nine years prior to catch. These results reflect differences in the nature and selectivity of the fishing gears used in the white perch fishery throughout the Bay. The Potomac results suggest that the Potomac white perch fishery targets larger, older fish, and that the JI does in fact represent year class strength.⁷⁰

Summers *et al.*⁸⁷ developed a categorical time series regression model to evaluate the effects of natural and anthropogenic environmental changes on the white perch stock in the Choptank River. Natural events apparently play the dominant role in determining the size of the Choptank white perch population. Two thirds of the variation in stock size for the period 1929-1985 could be explained by discharges of fresh water in April and May. Size of parental stock and sewage loadings lagged 2-3 and 9-10 years accounted for an additional 13% and 11% (respectively) of the variation.

Population Status and Fishery Landings

White perch support an important commercial fishery in Maryland and rank among the top ten species harvested in the State since 1920. From 1980-1985 white perch ranked from second to fourth both in pounds landed and dollar value. Because of their common occurrence and ubiquitous distribution, white perch are an extremely common by-catch in fisheries for other species. This fact makes it difficult to identify effort specifically targeted for this species. White perch are taken in nearly all types of fishing gear typically used on the Bay.⁷⁰

The minimum size of white perch caught in the Maryland commercial fishery is 8 inches (203 mm), i.e. about age V. Maryland white perch landings generally increased from 400,000-500,000 pounds in the late 1920's and early 1930's to a high of 2.2×10^6 pounds in 1969. Jones *et al.*³³ reported total catches for 1965-1973; the under-reported commercial landings are evident from the revised catch statistics from Casey *et al.*¹³ (Table 2).

Although commercial landings of white perch in Maryland have declined over the past 20 years, the white perch population does not appear to be suffering from over-exploitation. Thus, additional restrictions on either commercial or recreational fishing do not appear to be necessary.⁷⁰ But this conclusion assumes that reported

commercial landings accurately reflect population abundance and that total fishing effort and any change in that effort are known. Both of these assumptions are questionable. It has been very difficult to quantify white perch fishing effort because so much of the harvest has been taken as by-catch, particularly by the striped bass gill net fishery.

Increasing fishing restrictions on striped bass harvest, and the total moratorium on the Maryland striped bass fishery since 1985 have had a major impact on the white perch harvest. The catch declined by 44% from the previous ten-year average during the first two years of the moratorium.¹³ The commercial fishery for white perch operates primarily in late winter and early spring. From 1968-1979, a period of high harvests, 75% of the total annual harvest occurred in February, March, and April. During 1980-1985, when major changes occurred in the fishery due to changes in striped bass regulations, the percentage of the total annual harvest taken in those three months rose to over 90%.⁷⁰

During the mid- to late 1960's the largest commercial landings were from the Chester, Choptank, and Potomac Rivers and the upper Bay. In the early 1980's the Potomac was less important as a source of commercial landings than the other areas.⁸⁴

In Virginia, commercial white perch harvests were at historically high levels of about 800,000 pounds in the late 1940's and again in the late 1950's. Landings declined from the late 1950's through the mid-1960's, increased substantially in 1966, and declined throughout the 1970's and early 1980's.³³

White perch are an important recreational species, especially in the upper Chesapeake Bay and its tidal tributaries. They are common and are distributed among a variety of habitats, including inshore waters where they are available to anglers from shore or from small boats. Periodic fishing surveys in Maryland from 1965-1980 indicated that white perch accounted for 26-57% of the total hook and line catch of recreational anglers. Maryland's recreational catches of white perch were 1.2 and 0.75 x 10⁶ pounds in 1979 and 1980, approximately twice the commercial catch in 1979 and 70% of the commercial harvest in 1980.³³

LIFE HISTORY

Spawning

Chesapeake Bay white perch spawn from late March through early June; peak spawning activity occurs in April and May at water temperatures of 10-16°C;^{13,42,71} optimal spawning temperatures are 12-14°C (Table 3).⁷⁰

Spawning occurs in riverine and tidal fresh water as well as brackish water up to about 4.2 ppt salinity. Most spawn-

ing occurs in fresh water over fine gravel or sand;²⁷ optimal salinities range from 0-1.5 ppt (Table 3).³³ Spawning habitats in the Bay are shown in the Map Appendix. Not all eggs are released at once and ovulation may continue over a period of 10-21 days.⁴² Spawning distributions may vary from year to year in response to controlling environmental variables, primarily temperature and salinity.⁷⁰ Spawning generally occurs at depths of 1-6 m in estuaries.²⁷ Individual females are surrounded by several males, and eggs and sperm are spread randomly.

White perch eggs are small and spherical with a flattened attachment disc. Unfertilized eggs range from 0.7-0.9 mm; fertilized and water-hardened eggs average 0.92 mm and range from 0.75-1.04 mm.⁴² Generally eggs are demersal and attached in still water, but are pelagic in free-flowing streams and tidal waters.³⁹ They are not adhesive after water-hardening, which occurs within the first half-hour after ovulation.⁴² White perch eggs contain a large volume of yolk (0.14-0.16 mm)⁷⁰ and a prominent, amber-colored oil globule (0.0070-0.0081 mm).^{46,70} Hatching occurs after approximately 144 h at 11°C to 24-30 h at 20°C.²⁷

White perch have relatively high fecundity for fish their size. Fecundity estimates range from 5,000-320,000 eggs per female with an average of 40,000.²⁷ Regional estimates are: North Carolina 20,304-90,167; Chesapeake Bay 50,000-150,000; and Delaware Bay 280,000 (maximum).^{14,41,55}

Larvae

Newly hatched white perch larvae weigh approximately 35 µg, average 2.6 mm TL, and range in size from 1.7-3.0 mm. Larvae are tadpole-like, have unpigmented eyes and the mouth has not yet formed. The head deflects downward over a much enlarged yolk sac with a prominent anterior oil globule.⁴⁶ Hardy²⁷ provides detailed descriptions and drawings of white perch embryos, larvae, and juveniles. The yolk-sac (prolarval) stage lasts from 4-13 days.

First-feeding larvae averaged 3.45 mm standard length (SL), weighed approximately 19 µg, and had consumed at least 98% of their yolk reserves, and from 55-75% of their oil.⁴⁶ Rotifers and copepod nauplii were dominant prey of 3-4 mm white perch larvae from the Potomac River.⁸¹ Lesser numbers of copepodite stages of copepods and the cladoceran *Bosmina* were also consumed. *Bosmina*, copepodites, and adult copepods were dominant prey of 5-7 mm larvae; copepods, primarily adults, and cladocerans dominated diets of 8-15 mm larvae. Late larval and early juvenile white perch (16-24 mm) consumed adult copepods.

Depending upon food and temperature, white perch larvae grew from 0.01-0.28 mm d⁻¹ in laboratory experiments.⁴⁶ Well-fed larvae (800 rotifers L⁻¹) grew 0.05 mm

d^{-1} at 13°C, 0.20 mm d^{-1} at 17°C and 0.28 mm d^{-1} at 21°C. Survival rates of well-fed larvae ranged from 43-55% in these feeding experiments. Larvae fed initially at low food levels (50 rotifers L^{-1}) for as little as two days exhibited significantly reduced survival and growth during eight-day feeding experiments at all three experimental temperatures. Growth of white perch larvae at 13°C was slow under all food conditions; all larvae were < 4.0 mm SL after eight days.

At the two higher temperatures (17 and 21°C), survival rates of white perch larvae decreased by 60-80% with a four-day delay in high food levels, and decreased by 80-90% with an eight-day delay. Temperature and food concentration have important interacting effects on white perch during their first two to three weeks of life. Larvae hatched at 13°C were not as vulnerable to starvation, but they grew < 5% per day regardless of food level. Such larvae would be more vulnerable to predation for longer periods of time. At temperatures about 17°C, larvae could grow at > 20% per day if high food levels were available at first feeding. However, at 21°C, hatching success declined, and there was greater likelihood of starvation under suboptimal food conditions.⁴⁶

Growth rates of white perch cohorts from the Potomac River in 1987 ranged from 0.29-0.69 mm d^{-1} and averaged 0.40 mm d^{-1} .³² Cohorts of white perch larvae grew more slowly in their first 20 days post-hatch than subsequently. Cohorts that hatched before April 24, 1987 did not contribute to potential recruitment because of an episodic mortality of eggs and larvae caused by a drop in water temperature to < 10°C.

Instantaneous mortality rates of white perch cohorts ranged from 0.08-0.11 (average 0.09). White perch potential recruitment in the Potomac in 1987 was 10-100 times higher than that of striped bass.³²

Juveniles

The inshore zones of estuaries and creeks, generally somewhat downstream of the spawning areas, are the primary nursery areas for juvenile white perch during the first summer and fall. Juvenile white perch were present in the Choptank River during the last three sampling periods between May 21 and June 8, 1984. Initially the greatest numbers were caught at rm 49.1 (km 79), although during the last sampling interval a large downriver shift in abundance occurred coincident with heavy rainfall and a large rise in river flow.⁸

Growth rates of juvenile white perch are influenced strongly by environmental and habitat factors and differ markedly between regions and habitats, as indicated by white perch studies in Lake Ontario, the Delaware River, and the Connecticut River.^{44,55,80,91}

Adults

Manseuti⁴¹ estimated 100.3 mm SL and 105.5 SL as the median sizes at maturity for Patuxent River male and female white perch, respectively. All age II males in the Patuxent and all females above ~170 mm SL [200 mm fork length (FL)] were sexually mature. Approximately 67% of age II and 96% of age III female white perch from the Patuxent River were sexually mature.^{41,55}

Klauda *et al.*³⁴ summarized mean length-at-age data for 14 freshwater and estuarine white perch populations. Generally white perch from freshwater populations were larger, particularly in the younger year classes. Females age II and older tended to be larger than males, but the differences were not substantial. Mean lengths of male and female white perch from various estuarine populations are summarized in Table 4; length-weight relationships are listed in Table 5.

Although sex ratios of various estuarine and freshwater white perch populations vary widely, as a whole females generally outnumber males. Available data suggest different mortality rates for the sexes, but the differences have not been explained.⁷⁰

Generally younger age classes comprise the bulk of most white perch populations. Age classes III and IV dominated the James River population, and age classes II and III were most abundant in the York River.⁸⁵ Mean ages of Patuxent River males and females were 3.6 and 4.0 years respectively; 75% of the Patuxent white perch population was 4 years.⁴¹

White perch achieve most of their growth (in length) during the first several years of life. White perch from the York and James River reached ~35% of their age VII length during their first year.⁸⁵

White perch populations from various tributaries of the Chesapeake Bay may exhibit significantly different growth rates. Growth rates of white perch from Trappe Creek, a short, coastal estuarine creek in Talbot County, Maryland, were substantially greater than growth rates of white perch from the Choptank River.¹³ White perch from both populations were aged by examination of both scales and otoliths. Scale-based estimates differed significantly from otolith-based estimates for all age groups of white perch ($P < 0.001$); and for white perch with otolith ages IX-XVII ($P < 0.001$), but not for white perch with otolith ages I-VIII ($P = 0.134$). In the Choptank River, scale aging indicated high growth rates and short lifespans, whereas otolith aging indicated slower growth and greater longevity.

The age structure of white perch in the Choptank River (otolith method) reflected year class strength as measured by the Choptank JI (Table 1). The age distribution of

WHITE PERCH

otolith-aged fish collected in 1987 was correlated with the JI ($r^2 = 0.77$; $P = 0.01$) for ages V to XII white perch (1976-1982 year classes). The JI accounted for most of the variation in otolith-aged fish collected in 1986¹³ (1975-1982 year classes; $r^2 = 0.99$; $P = 0.0001$). These results indicated that scales underestimated the age of older white perch from the Choptank and gave biased age estimates after age VIII. Thus, age distributions of older white perch, along with growth and mortality rates, derived from scale-aged fish are suspect.¹³

Annual mortality rates (calculated from age frequency distributions of scale-aged fish) for adult and subadult white perch typically range from ~0.57-0.69. White perch mortality was greater in the James River than in the York River. White perch males after age IV suffered 69% mortality (0.69 ± 0.07 , 95% CI); females after age VI suffered similar mortality rates (0.68 ± 0.07). In the York River, annual mortality rates for age III and older males were 0.59 ± 0.05 ; and for females < age V, 0.57 ± 0.06 .⁸⁵ However, the annual mortality rate of white perch from the Choptank River was 0.15 (aged by otolith examination).¹³ As above, the scale method apparently gives biased age estimates, especially for older age classes. This problem would result in overestimates of annual mortality.

ECOLOGICAL ROLE

Larval white perch are zooplankton predators, and in turn, are prey for juvenile white perch and other species. Larval white perch initiate feeding on rotifers and copepod nauplii, cladocerans, and copepodites. Adult stages of copepods become increasingly more important in the diets of older larvae.⁸¹ Juvenile white perch prey on benthic invertebrates; insect larvae are a majority prey of freshwater populations. Prey availability apparently limits growth of juveniles and older white perch in some populations, at least, during times of high abundance.

Juvenile white perch (< 150 mm) from the Choptank River fed on mysids and other benthic organisms; larger white perch fed almost exclusively on tunicates (sea grapes). Juvenile white perch consumed striped bass eggs and larvae in laboratory experiments.^{49,56} Juveniles consumed approximately two striped bass eggs per 15 minutes. Predation rates increased to approximately 15 striped bass larvae (7-12 days post-hatch) per 15 minutes and then declined. High turbidity significantly increased the predation rate on yolk-sac larvae.⁴⁵

Juvenile bluegills can be effective predators on larval white perch. They captured all larval white perch, 3-6 mm SL in laboratory predation experiments.^{45,47} Maximum predation was 10 larvae per 15 minutes at a prey density of 0.3 larvae L⁻¹, a realistic density of larval white perch in Chesapeake Bay spawning and nursery areas. Susceptibility of white perch larvae to capture declined by 21%

per mm length for 6-14 mm white perch larvae. Percentage of larvae killed decreased to 30% at 12 mm SL and dropped to 18% at 14 mm SL. The addition of similar-sized, alternative prey, a cladoceran, resulted in 10-90% reduction in predation rates on white perch larvae by juvenile bluegill. No selection was observed either for the white perch or the cladoceran. Both were consumed in proportion to their abundance.^{45,47}

White perch larvae co-occur with many potential fish predators in tidal fresh waters, including juvenile white perch, alewife and blueback herring, menhaden, bay anchovy, catfishes, eels, striped bass, yellow perch, sunfish, and largemouth bass.⁴⁷ Juvenile white perch in estuarine habitats are prey for yearling and older striped bass, adult white perch, and probably bluefish.⁴

Subadult and adult white perch are benthic predators. Older white perch become increasingly piscivorous. Age I and older white perch from Oneida Lake consumed insect larvae and crustaceans.¹ Insect larvae and fishes were the principal foods of white perch from the Bay of Quinte. Dipteran larvae, especially chironomids, were the most important insect prey. Fish - yellow perch, white perch, and johnny darters - constituted 35% of the diet of 7 inch (178 mm) white perch and 70% of the diet of 8-10 inch (216-254 mm) white perch.

White perch captured on their spawning grounds in a northwest Ohio tributary of Lake Erie were voracious predators of fish eggs. The eggs of walleye, white perch, and white bass mixed with detritus comprised nearly 100% of their diet while on the spawning grounds.⁷³

HABITAT REQUIREMENTS

Water Quality

Suitable water quality for white perch eggs, larvae, and juveniles - the most sensitive life stages - and for adults are summarized in Table 3.

Dissolved Oxygen

White perch concentrate in areas with DO of at least 6 mgL⁻¹. In a recent intensive trawl survey, no white perch were collected where DO was < 4 mgL⁻¹ in the Patuxent River or < 3 mgL⁻¹ in the Choptank River. Most white perch in both rivers were taken from areas with DO ≥ 6 mgL⁻¹. Likewise, in the mainstem Chesapeake Bay, the largest collections of white perch occurred in areas with > 7.0 mgL⁻¹ DO. White perch occurred in only one sample in an area of < 5.5 mgL⁻¹ DO.⁷³

A minimum DO of 5 mgL⁻¹ is recommended for all life stages of white perch (Table 3).³³ Only two laboratory studies have examined the effects of low DO on young-of-year and adult white perch. Young-of-year white perch suffered 40% mortality when exposed to DO of 0.5-1.0

mgL⁻¹ for 19 h over a temperature range of 6.7-28.3°C.¹⁶ Adult white perch avoided waters with DO < 35% saturation over a temperature range of 8-21°C.⁵²

Salinity

Few studies have examined the effects of salinity on various life stages of white perch. Optimal salinity for white perch eggs ranges from fresh water to 2 ppt,³³ though a salinity range of 0-10 ppt did not significantly affect percent hatch of water-hardened eggs in laboratory experiments.⁶² Most (99%) of white perch eggs collected in the upper Chesapeake Bay were collected in fresh water.¹⁷

White perch larvae and juveniles are found in fresh and low salinity water of 0-8 ppt. Larvae and juveniles prefer salinities < 1.5 ppt and < 3 ppt, respectively,⁸⁶ although both larval and juvenile white perch have been collected in salinities up to 13 ppt.^{17,86} Eighty-eight percent of larval and juvenile white perch from the upper Chesapeake Bay were collected in fresh water; 9% were collected at 1 ppt.¹⁷

Adult white perch are found in salinities from 5-18 ppt.⁸⁶ The greatest catches of white perch in the Patuxent River during the 1989-90 trawl survey occurred in 0-3 ppt and in 12-15 ppt. However, few trawl samples were taken between 4-11 ppt. Likewise, white perch rarely were collected from localities in Chesapeake Bay where salinity exceeded 9 ppt.⁷³

Temperature

White perch eggs hatch in ~24-30 h at 20°C, to 144 h at ~11°C. Water temperatures < 10°C caused significant mortality of white perch eggs.²⁷ The relationship between time to 50% hatch and water temperature is:

$$t = 686.900e^{-0.1402T}$$

where t = time in h and T = temperature (°C).

Optimal hatching of white perch eggs occurs at 12-14°C (Table 3).^{62,70} Temperature decreases of 4-5°C were lethal to developing eggs; a sudden decrease of 2-3°C resulted in egg mortality.^{2,27} Incubation time of white perch eggs in laboratory studies decreased by a factor of 3 from 13-21°C, but the reduced incubation time at higher temperature was offset by a decline in percent hatch of about 60%. Percent hatch was approximately 80% at 13°C, 60% at 17°C, and only 20% at 21°C.⁴⁶

Maximum length of white perch larvae at hatch occurred at temperatures of 16-18°C.⁶² Young-of-year white perch acclimated at 30°C or greater selected water temperatures less than or equal to acclimation temperatures. Juvenile white perch acclimated at temperatures of 6, 12, 18, 24, 30, and 33°C selected water temperatures ranging from 15.2-31.0°C, depending upon acclimation temperatures.²⁴ Southern populations of young-of-year white perch se-

lected higher temperatures than more northern populations. Preferred temperatures ranged from 31.6-32.5°C for North Carolina populations, 28.9-30.6°C for Maryland populations, and 29.2-29.6°C for New Jersey populations.²³

Juvenile white perch can acclimate to increasing water temperatures. Eight percent survival occurred when juveniles were exposed to 30.6°C for 24 h after three days exposure to increasing water temperatures, beginning at 20°C.¹⁶ However, juveniles acclimated to 21-26°C suffered significant mortality when exposed to temperature increases of 8.4°C or greater for over 15 minutes.⁵¹

Temperature preference in adult white perch depends both upon acclimation temperatures and latitude of the population. White perch acclimated at 5, 8, and 10°C in 26-27 ppt salinity preferred water temperatures of 23, 22.8, and 21.5, respectively.⁸⁸ White perch from the Delaware River preferred a maximum summer temperature of 32.2°C;⁵¹ white perch from New Jersey avoided 32°C water in laboratory experiments;²¹ and white perch from the Hudson River selected a lower temperature, 27.8°C, and avoided temperatures < 9.5°C and > 34.5°C.⁸⁹

Suspended Sediments

Suspended sediment concentrations of 100 and 500 mgL⁻¹ delayed hatch of white perch eggs by 4-6 h.⁷⁶ Continuous exposure of white perch eggs to suspended sediment concentration of 1000 mgL⁻¹ significantly reduced hatching success.³ Although a 12 h exposure to 50-5250 mgL⁻¹ of suspended sediments did not affect percent hatch of white perch eggs, development was slowed significantly at suspended sediment concentrations > 1500 mgL⁻¹.⁶³ High concentrations of suspended sediments, 2000-3250 mgL⁻¹, reduced egg development to 80% of controls.⁵⁷

Deposition of sediment on white perch eggs is apparently more important than suspended sediment concentrations. Covering white perch eggs with a 1.1 mm sediment layer resulted in 100% mortality. No significant reduction in hatching success occurred when a sediment layer less than one-half egg diameter was deposited around eggs;⁷⁸ however, sediment layers which extended over halfway up and to the top of the eggs resulted in greater than 50% mortality. Most deaths occurred in the late morula and early gastrula stages: times of rapid cell division when high rates of gas exchange through the chorion are needed.⁶³

White perch larvae, juveniles, and adults are affected adversely by natural sediment concentrations typically found in estuaries during floods, dredging, and dredge spoil disposal. White perch larvae are more sensitive to suspended solids than are adults.⁸³ Four sediment concentrations ranging from 1,557-5,380 mgL⁻¹ resulted in 15-19% mortality of one day post-hatch larvae during

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one-day exposures and 23-49% mortality during two-day exposures.⁶³ Sherk *et al.*⁸³ considered young-of-year white perch highly sensitive to sediment concentrations. Young-of-year white perch suffered 100% mortality after a 20 h exposure to 750 mgL⁻¹ suspended sediments at 18°C.

pH

Little is known about the effects of pH on various life stages of white perch. Klauda³⁵ proposed that reproduction would be significantly reduced if white perch were exposed for seven days to pH 6.5-6.7, in association with a total monomeric aluminum concentration of 25 µgL⁻¹ and dissolved calcium concentration of 2 mgL⁻¹. He also suggested that short duration (< 48 h) exposure to pH 6.0 could severely reduce survival of white perch larvae. Stanley and Danie⁸⁶ assumed that adult white perch tolerate a pH range of 6.0-9.0.

Shear

Shear stress can cause mortality of eggs and larvae by creating excess rotation or deformation. However, LS₅₀ (median shear that would kill 50% of test animals in a given time period) ranged from 425-415 dynes cm⁻² for one-minute exposures of white perch eggs and larvae, respectively. The LS₅₀ was 120 dynes cm⁻² for a 20 minute exposure of white perch eggs, and 125 dynes cm⁻² for a four-minute exposure of white perch larvae. These shear forces are much greater than the maximum shear force against the sides of the Chesapeake and Delaware Canal (13.8 dynes cm⁻²) which is operative over only a thin boundary layer (20 mm), and also are greater than shear forces generated by a cargo ship (~79 dynes cm⁻²).⁵⁹ White perch eggs and larvae can be killed, however, by the shear forces found in the intake structures of power plants and other large industrial users of water.

Structural Habitat

Substrate

Although commonly found near underwater structures (e.g., piers, brush and vegetation), white perch apparently prefer areas with mud, sand or clay bottoms with little or no cover.⁷³

Depth

Larval white perch begin moving into shallow shore zones, less than 1 m deep, at about 8 mm TL.⁴² Young-of-year white perch prefer shallow inshore zones of estuaries and creeks, generally somewhat downstream from spawning areas. Although young-of-year white perch occasionally may venture into deeper waters during daylight, they return to protected beach and shoal waters at night and during periods of rough water.⁸⁶ During the summer, older white perch apparently prefer depths of 4.6-9 m during the day and move inshore to ~1 m at night. White perch overwinter in deeper channel waters usually

at 12-18 m, although they have been taken from areas as deep as 42 m.

White perch concentrate in relatively small areas during winter months, which facilitates sampling. Preliminary results of the Patuxent River 1990 winter trawl survey indicate that during January and February white perch should be sampled in depths > 8 m at temperatures of 2-5°C and salinities ≤ 5 ppt.⁷³

Avoidance Responses

Various devices including bubble curtains and strobe lights have been examined in attempts to decrease the numbers of young-of-year fish entrained into power plant intake channels and impinged on screens at entrances to intake structures. White perch avoided bubble curtains at moderate turbidity (45 NTU) but were attracted to them either in clear water or at high turbidity.⁵⁰ They also apparently are attracted to bubble curtains at flow rates of 0.2-0.5 m s⁻¹.⁷⁴ White perch partially avoided strobe lights in low flow experiments and decreased the use of strobe-lit areas by 10-36% at a flow rate of 0.2 m s⁻¹; however, the avoidance response decreased at higher velocities (12-22% avoidance at 0.3 m s⁻¹ and 8-24% avoidance at 0.5 m s⁻¹).

At low currents (0.2 m s⁻¹), light-acclimated white perch avoided strobe lights at flash frequencies of 120 and 300 per minute, whereas dark-acclimated fish avoided strobe lights only at higher flash frequencies (300 and 600 per minute).⁷⁴ High turbidity apparently also interferes with the avoidance response of white perch to strobe lights. McInnich and Hocutt⁵⁰ found 40% avoidance to strobe lights at turbidity of 102-138 NTU.

SPECIAL PROBLEMS

Contaminants

The effects of contaminants on various life stages of white perch are summarized in Table 6.

Chlorine and ozone

The effects of chlorine and ozone on white perch have received more study than those of any other contaminants. When comparing chlorine toxicity data, the terms total residual chlorine (TRC), chlorine produced oxidants (CPO), and total residual oxidants (TRO) are equivalent.

White perch eggs maintained at 15°C in 2.5 ppt salinity suffered 50% mortality after 76 h at a TRC concentration of 0.27 mgL⁻¹.⁶⁰ Fifty-five percent of white perch eggs exposed to 0.35 mgL⁻¹ TRC did not develop beyond the gastrula-germ ring stage. White perch eggs suffered 100% mortality at 0.55 mgL⁻¹ TRC.⁶¹ Length of white perch larvae at hatch decreased with increasing TRC. Length of larvae at hatch was 2.5-5.5% less than length of control larvae at

concentrations $\geq 0.10 \text{ mgL}^{-1}$ TRC.⁶¹ Mortality of white perch larvae was a function of TRC and exposure duration.^{11,24,26}

Total chlorine was more toxic to adult white perch in 1 ppt salinity than in fresh water. Ninety-six h LC₅₀ values were 0.10 mgL^{-1} in 1 ppt and $0.61\text{--}0.87 \text{ mgL}^{-1}$ in fresh water. Conversely, ozone was more toxic to adult white perch in fresh water than in 1 ppt salinity (Table 6). However, adult white perch were more sensitive to both ozone and total chlorine (as indicated by avoidance concentrations and "cough" responses) in low salinity waters than in fresh water (Table 6).⁵⁴

Other studies on adult white perch reported similar 96 h LC₅₀ or TL₅₀ concentrations, ranging from $0.15\text{--}0.22 \text{ mgL}^{-1}$ TRC or CPO depending upon experimental temperatures and salinities.^{5,6,22,65} Chlorine-produced oxidants lowered blood pH in adult white perch in fresh water and greatly increased gill carbonic anhydrase and hematocrit;^{5,6} at 14 ppt, both blood pH and hematocrit decreased.⁷

An inverse relationship exists between both temperature and salinity and the concentration of free residual chlorine (FRC) required to elicit an avoidance response by adult white perch.⁵² Likewise, an inverse relationship exists between the percentage FRC of total chlorine and the concentration of total chlorine required to bring about an avoidance response, suggesting that FRC is more toxic than other components of TRC.

The acute toxicity of ozone produced oxidants (OPO) to adult white perch (96 h LC₅₀ = $0.20\text{--}0.22 \text{ mgL}^{-1}$)^{69,72} is similar to that of TRC or CPO. Exposure to OPO 0.1 mgL^{-1} results in histological changes on white perch gill surfaces within 24 h.^{72,69} Additionally, OPO concentrations 0.10 mgL^{-1} increased hematocrit, and OPO concentrations 0.15 mgL^{-1} reduced blood pH.⁶⁹

Petroleum

The toxic effects to adult white perch of No. 2 and 4 fuel oils, an oil collection agent, a dispersant, and mixtures of these substances have been examined⁶⁸ (Table 6). The toxicity of the dispersant (96 h TL₅₀ = 4.2 mgL^{-1}) was 8-9 times greater than the toxicity of either fuel oil (96 h TL₅₀ $31\text{--}37 \text{ mgL}^{-1}$), whereas the oil collecting agent was not toxic to white perch (96 h TL₅₀ > 500 mgL^{-1}). Toxicity of the fuel oils increased greatly when the dispersant was added, due to partial solubilization of the oils (96 h TL₅₀ $1.0\text{--}1.4 \text{ mgL}^{-1}$). Fuel oil toxicities were not significantly affected by the addition of the collecting agent.

Trace Metals

Rehwolt *et al.*⁶⁷ examined the effects of three heavy metal ions on adult white perch acclimated at 17°C. Adult perch were twice as sensitive to copper (96 h TL₅₀ = 6.2 mgL^{-1})

as they were to either nickel (96 h TL₅₀ = 13.6 mgL^{-1}) or zinc (96 h TL₅₀ = 14.3 mgL^{-1}).

White perch larvae collected from the Potomac River in 1985 were analyzed for trace metals. At the beginning of May, white perch larvae had very high aluminum concentrations ($\sim 9,000 \text{ mg g}^{-1}$ dry weight), although by the end of May the mean larval aluminum concentration had fallen to about 300 mg g^{-1} . Body concentrations of both copper and lead initially fell through the first half of May, but an upturn in concentrations occurred during the latter half of May.⁹⁶

White perch apparently accumulate abnormally high levels of copper in their livers, probably as a result of an inherited metabolic defect. Copper concentrations in the livers of white perch collected from the Bush, Rhode, Wye, and Magothy Rivers generally increased with age and often exceeded $1000 \mu\text{g g}^{-1}$ wet weight. This propensity to accumulate copper does not seem to be associated with environmental contamination, because white perch were collected from widely separated regions, and copper concentrations in the livers of striped bass and pumpkin-seed sunfish collected from the same areas averaged $3 \mu\text{g g}^{-1}$ wet weight.⁹

Contaminated Natural Waters

Adult white perch suffered deleterious effects from a 30-day laboratory exposure to Baltimore Harbor water.⁵⁸ Sublethal physiological effects on white perch blood cells included increased numbers of thrombocytes and decreased numbers of neutrophils and basophils. Biochemical effects included changes in the levels of three enzymes: lactate dehydrogenase (LDH), acetylcholinesterase, and catalase. Poor water quality resulted in increased LDH activity in white perch blood serum. Organophosphorus pesticides were responsible for the reduced acetylcholinesterase activity within white perch brains, whereas liver damage from metal ions resulted in decreased catalase levels.

Eutrophication

Monthly trawl catch data from 1965-1968 and 1988-1989 were compared for two sites in the Patuxent River: an upper estuary site, Benedict Bridge at rm 20 (km 32) and a mid-estuary site, Broomes Island at rm 12 (km 19). Fish community structure changed over the two decades between the surveys. The area around Broomes Island no longer is acceptable habitat for white perch and striped bass.⁹⁴ White perch dominated trawl catches at Benedict Bridge in 1965-1968, comprising 54% of the catch. In 1988-89 white perch still dominated, making up 51% of the total catch. At Broomes Island white perch was the dominant species in 1965-68, comprising 82% of the total catch. Striped bass, hogchokers and harvestfish accounted for an additional 11% of the total catch. But in 1988-89, white perch and striped bass were extremely rare

at Broomes Island. Trawl catches were dominated by spot, which can tolerate lower DO than most fishes in the Bay (see SPOT: **Habitat Requirements**, this volume), bay anchovies, and weakfish, species indicative of more eutrophic waters.

In 1965-68 species diversity at both stations was lowest in January and highest in late June and early July. The same seasonal cycle in species diversity occurred at Benedict Bridge in 1988-89, but at Broomes Island there was a three-month phase shift in species diversity from 1965-68 to 1988-89. By 1988-89, the lowest species diversity was in April, and the highest diversity was in October.⁹⁴ This seasonal shift in species diversity is another indication of deteriorating water quality in the warm months in the Broomes Island area.

The Patuxent estuary has changed greatly in the past 50 years as a result of increasing nutrient loads and eutrophication.¹⁵ Chlorophyll *a* concentrations in surface waters at Broomes Island increased from 30-40 μgL^{-1} during May-July 1968 to 17-138 μgL^{-1} in 1978. The DO in bottom waters in the vicinity of both Broomes Island and Benedict was much lower in 1977-79 than in 1936-40.²⁸ During July-September, 1988, bottom DO < 2 mgL^{-1} was found in depths as shallow as 4.2 m in this portion of the estuary.⁹⁴ Changes in fish community structure distribution and abundance in the Patuxent estuary over the past two decades are symptoms of eutrophication.

The increase in the extent of anoxic and hypoxic bottom waters and the earlier onset of hypoxia may affect the overwintering habitats of white perch and other species in Chesapeake Bay. White perch overwinter in the deep holes just south of the Bay Bridge. Bottom DO in these deep waters had dropped to 3 mgL^{-1} by the beginning of April 1990 (personal communication: Robert Magnien, Maryland Department of the Environment).

Dredged Material Disposal

Deep areas of the Bay have been proposed as dumping areas for "clean" dredged material. The problem of disposal of dredged material is becoming increasingly acute as existing disposal areas are filled. Any increased biochemical oxygen demand (BOD) associated with disposal of dredge spoil could exacerbate the anoxia problem and degrade or destroy valuable white perch overwintering habitat.

RECOMMENDATIONS

Increase Dissolved Oxygen

Dissolved oxygen concentrations of at least 5 mgL^{-1} are required for all life stages of white perch. Increasing bottom DO in summer to at least 5 mgL^{-1} in the oligohaline (0.5-5 ppt salinity) and mesohaline (5.1-18 ppt) portions of the Bay will increase suitable summer habitat for white

perch. Overwintering habitats of white perch in Chesapeake Bay are limited by the extent of bottom waters with DO < 5 mgL^{-1} . Earlier onset of severe hypoxia in the deep overwintering habitats would eliminate use of these habitats in late winter and early spring.

Protect Deep Hole Habitats

Disposal of dredge spoil in deep portions of Chesapeake Bay should be avoided because it could damage or destroy valuable overwintering habitats for white perch by increasing BOD.

Improve Stock Statistics

Stock-specific growth and mortality rates are needed to develop a realistic White Perch Fishery Management Plan. Mortality rates should not be estimated from simple, static catch curves. Growth rates are highly variable, and in stunted populations especially, a small length increment easily can include fish of different ages. Also, scales apparently underestimate the age of older white perch, at least in some populations. Validation studies such as oxytetracycline labeling of fish and long-term holding experiments are needed to test aging techniques (scale aging vs. otolith aging) for white perch.

Consider Regional Management of Self-Contained Fisheries

From a biological perspective, white perch stocks in the Upper Bay, Patuxent, Potomac, James, and York Rivers should be managed separately because of the strong regional nature of the fishery and the fact that stocks in the lower western shore tributaries essentially are self-contained. The feasibility of a regional management scheme should be examined.

Better statistics are needed on the magnitude of recreational catches of white perch in the upper Bay and various tributaries.

CONCLUSION

White perch is one of the most important species in the Bay for both commercial and recreational fishing. Although the stock does not appear to be suffering from overfishing, it is difficult to be sure because so much white perch is taken as by-catch in other fisheries (especially striped bass). The by-catch aspect makes it difficult to determine the total fishing effort for white perch. Maryland's ban on striped bass fishing has contributed to reduced fishing effort, and hence, a decline in commercial white perch landings in recent years. Steps should be taken to increase DO and to improve statistics on the magnitude of recreational catches of white perch in order to help this important species thrive in the Bay.

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Table 1. Average number of young-of-year white perch per seine haul by year and area (unpublished data: MDNR).

Year	Head of Bay	Potomac River	Choptank River	Nanticoke River	Yearly Average
1958	7.4	9.6	10.8	9.1	9.0
1959	8.8	103.0	10.5	8.0	35.3
1960	2.9	96.8	156.9	86.3	77.1
1961	8.8	51.5	27.8	73.8	37.8
1962	5.6	28.7	31.2	15.3	19.3
1963	17.3	7.0	33.3	11.2	15.8
1964	24.9	29.6	2.7	23.9	22.2
1965	12.9	29.6	3.2	21.3	11.3
1966	58.0	18.2	41.2	35.1	38.1
1967	4.5	6.4	23.4	54.5	17.6
1968	25.5	13.2	11.0	36.1	20.9
1969	72.8	22.4	13.4	56.8	43.0
1970	76.9	58.3	23.9	70.7	60.2
1971	19.0	29.0	13.4	17.8	21.0
1972	13.7	31.7	6.3	10.7	17.5
1973	13.5	24.1	0.7	2.4	12.5
1974	4.6	4.5	4.2	6.8	4.9
1975	11.0	14.7	7.9	9.5	11.4
1976	5.5	4.6	0.6	2.9	3.9
1977	16.2	12.8	0.8	0.5	9.5
1978	25.7	71.8	6.8	28.9	37.5
1979	14.2	3.0	11.0	2.1	7.8
1980	19.4	12.8	1.0	3.8	11.1
1981	7.4	1.3	9.6	7.0	5.8
1982	32.3	6.6	9.2	7.7	15.5
1983	7.2	4.5	16.8	11.3	8.8
1984	20.6	23.7	11.5	40.2	23.5
1985	1.2	3.2	18.6	6.5	6.0
1986	31.7	7.8	6.9	15.3	16.6
1987	0.5	10.2	77.4	56.6	27.8
1988	19.8	1.3	1.1	6.5	4.9
1989	25.9	11.9	46.7	60.4	31.5
32-year mean	19.2	23.6	20.0	25.0	21.4

Table 2. Total Commercial White Perch Landings in Maryland.

Year	Landings (lbs.)	
	Jones et al. 1988 ³³	Casey et al. 1988 ¹³
1965	1,449,900	1,759,866
1966	1,747,300	2,395,009
1967	1,246,900	1,742,562
1968	1,795,800	2,197,405
1969	2,152,500	2,703,150
1970	1,661,800	1,937,926
1971	1,507,700	2,008,715
1972	1,226,900	1,420,200
1973	762,600	1,013,900

Maryland catches declined to 650,000-840,000 pounds from 1974-1984 with the exception of harvests of 1.2 and 1.1 x 10⁶ pounds in 1978 and 1980, respectively.¹³

WHITE PERCH

Table 3. Suitable water quality for various life stages of white perch. Optimum values are in **bold face**.
na: not available.

Life stage	Temperature ^{27,33,62,70} °C ^a	Salinity ^{18,19,27} ppt	pH ²⁷	Dissolved oxygen ²⁷ mgL ⁻¹	Suspended solids ^{32,35} mgL ⁻¹
Eggs	12-20 12-14	0-1.5	6.5-8.5	> 5	< 100
Larvae	12-20	0-1.5	6.5-8.5	> 5	<< 500
First-feeding larvae	15-20				
Juveniles	10-30	0-3 ^b	7-9	> 5	<< 500
Adults	10-30	5-18	na ^c	> 5	< 500

^a Optimum temperature range is dependent upon the acclimation temperature.

^b Summer; somewhat higher salinities thereafter.

^c Theoretical pH range of 6.5- < 9.^{35,86}

Table 4. Calculated length (mm) at age for white perch.

Location	Sex	Age Group										Reference
		I	II	III	IV	V	VI	VII	VIII	IX	X	
Patuxent River, Maryland	M	90	134	158	175	190	206	231	241	249		41
	F	93	141	167	184	199	220	237	251	265	287	
James River, Virginia	M	77	119	146	168	183	199	218				85
	F	77	122	151	174	191	205	220	236	253	262	
York River, Virginia	M	81	116	141	167	186	204	235				85
	F	78	118	146	171	190	210	228	247	260	270	
C & D Canal ^a	M	79	113	140	160	178	195	216	243	249	254	31
	F	81	116	139	158	177	188	207	204	230		
Delaware River ^b	M	83	131	154	169	182	192	204	203			91
	F	84	134	158	174	185	195	201	209			
	M	75	121	144	161	182	202	251				66
	F	76	122	145	163	185	208					
Hudson River, New York	M	85	144	174	187	198	211	223				4
	F	88	149	182	200	211	219	230				
	M	71	121	148	163	175	184	195	203			38
	F	73	123	151	167	180	195	212	226	260		

^a and adjacent waters.

^b near Artificial Island

Table 5. Length-weight relationships for various estuarine white perch populations. W = weight in g; SL = standard length in mm; FL = fork length in mm.

Population	Sex	N	Equation	r ²	Reference
Patuxent River	F	888	$\log(W) = -4.814 + 2.123 \log(SL)$		41
	M	580	$\log(W) = -4.611 + 3.023 \log(SL)$		
James River	F	323	$\log(W) = -5.374 + 3.302 \log(FL)$	0.98	85
	M	290	$\log(W) = -5.199 + 3.182 \log(FL)$	0.98	
York River	F	347	$\log(W) = -5.008 + 3.161 \log(FL)$	0.98	85
	M	385	$\log(W) = -5.172 + 3.190 \log(FL)$	0.97	
Hudson River	F		$\log(W) = -4.738 + 3.099 \log(SL)$	0.96	4
	M		$\log(W) = -2.262 + 1.925 \log(SL)$	0.71	

Table 6. Effects of contaminants on white perch. Life stages: E = eggs; L = larvae; J = juveniles; A = adults.

Substance	Life stage	Salinity ppt	Temperature °C	Effect	Concentration mgL ⁻¹	Reference
chlorine (TRC)	E			76 h LC ₅₀	0.27	60
	E	2.5	15	mortality ^a	0.55	61
	L			24 h LC ₅₀	0.31	60
	L			growth ^b	> 0.5	61
	L			see text for chlorine-temperature interactions.		
	L	1.5	18	see text for chlorine-temperature interactions.		
	A		15	96 h LC ₅₀	0.21	22
	A		25	96 h LC ₅₀	0.15	22
	A	0-7	0-27	avoidance	0.04-0.35 ^c	53
	A	0-8	4-28	avoidance	0.21	65
	A	0	14.2-16	sublethal (30 min.)	1.35	6
	A	2.7	16.9	96 h TL ₅₀	0.22	65
	A	1	14.5	96 h LC ₅₀	0.10	54
	A	0	11	96 h LC ₅₀	0.87	54
	A	0	19	96 h LC ₅₀	0.69	54
	A	0	22	96 h LC ₅₀	0.61	54
	A	0	26	96 h LC ₅₀	0.74	54
chlorine (NaOCl)	A			24-48 h LC ₅₀	2.8 ^d	37
chlorine (free residual)	A	0.5-7.0	4-27	avoidance	0.03-0.16 ^c	52
	A	0.5-7.0		avoidance	0.10	65
ozone	A	1-2.5	20-27	avoidance	0.07 (mean)	54
	A	0	6-25.8	avoidance	0.11 (mean)	54
	A	0	11	96 h LC ₅₀	0.37	54
	A	0	19	96 h LC ₅₀	0.26	54
	A	0	21	96 h LC ₅₀	0.22	54
	A	0	27	96 h LC ₅₀	0.29	54
	A	0	6.5-23	"cough" response	0.09-0.17	54
	A	1	14.5	96 h LC ₅₀	> 0.66	54
	A		15	96 h LC ₅₀	0.22	72
ozone (OPO)	A		15	24 h sublethal ^e	0.01	69
	A		15	96 h LC ₅₀	0.20	69
	A		15	sublethal ^f	0.01-0.15	69
	A		19	24-96 h TL ₅₀	41.6-37.2	68
No. 2 fuel oil with dispersant (LAS)	A		19	24-96 h TL _m	1.4-3.0	68
No. 4 fuel oil with LAS	A		19	24-96 h TL ₅₀	31.0-32.0	68
LAS	A		19	24-96 h TL _m	1.0-1.4	68
LAS	A		19	24-96 h TL ₅₀	4.2-6.1	68
fuel oil collecting agent	A		19	24-96 h TL ₅₀	≥ 500	68
copper	A		17	48 h TL ₅₀	8.0	67
	A		17	96 h TL ₅₀	6.2	67
zinc	A		17	48 h TL ₅₀	10.2	67
	A		17	96 h TL ₅₀	14.3	67
nickel	A		17	48 h TL ₅₀	16.2	67
	A		17	96 h TL ₅₀	13.6	67

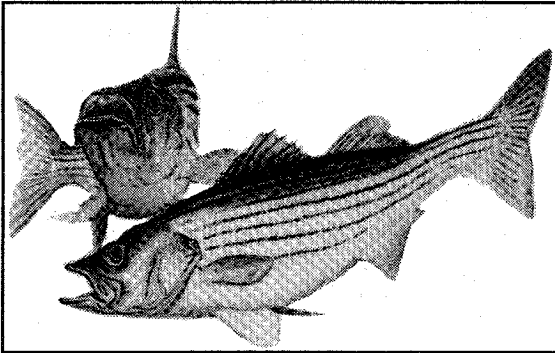
^a Prevented egg development past gastrula stage.^b Larval length decreased by 2.5-5.5%.^c Tests involved temperature-salinity-chlorine interactions.^d Single 2 h dose of NaOCl.^e Histologic changes on gills within 24 h of exposure to ≥ 0.01 mgL⁻¹ OPO.^f Blood and tissue effects at 0.01-0.15 mgL⁻¹ OPO.

STRIPED BASS

Morone saxatilis

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The striped bass is a large anadromous fish found along the entire East Coast of North America. Most of the coastal migratory stock originates in Chesapeake Bay. Striped bass spawn in spring in tidal freshwater areas just above the salt wedge. Most juvenile striped bass remain in their natal areas for the first two years of life. Older fish migrate from the Bay into the coastal Atlantic Ocean. Striped bass are voracious predators, mostly on fish. Early life stages are important prey for other species.

Striped bass have been one of the most sought-after commercial and recreational finfish in Chesapeake Bay. A long term decline in striped bass stocks began in the mid-1970's, primarily because of overfishing. Sustained poor recruitment and low stock abundance led to a complete closure of Maryland and Virginia fisheries by the mid- to late 1980's. In response to increased stocks and stronger recruitment, limited commercial and recreational fisheries were reopened in 1990.

There is increasing concern that low dissolved oxygen (DO) in the deeper water of the upper Chesapeake Bay and in other areas has eliminated much of the summer habitat of adult and subadult striped bass. Acidity and contaminants in spawning habitats have been associated with mortality of striped bass larvae in the Choptank, Nanticoke and Potomac Rivers.

INTRODUCTION

Striped bass has been well known since colonial days, undoubtedly due to its great abundance and availability. Captain John Smith wrote:

"The Basse is an excellent fish, both fresh and salte . . . They are so large, the head of one will give a good eater a

*dinner, and for daintinesse of diet they excell the Marybones of Beefe. There are such multitudes that I have seene stopped in the river close adjoining to my house with a sande at one tide as many as will loade a ship of 100 tonnes".*¹¹²

William Wood in his *New England's Prospect*, published in 1634, describes how to catch a really large bass:

*"The Basse is one of the best fishes in the countrey, . . . the way to catch them is with booke and line: the fisherman taking a great cod-line, to which he fastneth a peece of lobster, and throwes it into the sea, the fish biting at it he pulls her to him, and knockes her on the head with a stick . . . the English at the top of an high water do crosse the creekes with long seanes of Basse netts, which stop in the fish; and the water ebbing from hem they are left on the dry ground, sometimes two or three thousand at a set . . ."*²⁴¹

Striped bass and codfish were the first natural resources in Colonial America subject to conservation measures enacted by statute. In 1639, the General Court of the Massachusetts Bay Colony passed a law that neither fish could be sold as fertilizer. But the catch increased, and by 1776 New York and Massachusetts had passed laws prohibiting sales of these fish in winter months.¹³

The first public school in the thirteen colonies was made possible in part through funds derived from the sale of striped bass. An act of the Plymouth Colony in 1670 required that all income accrued annually to the Colony from the fisheries at Cape Cod for striped bass, mackerel, and herring be used for a free school in some town of the jurisdiction.¹⁸⁴

The presence of the striped bass on the Great Seal of Maryland indicates the high esteem in which Marylanders hold the fish, colloquially known as rock or rockfish.¹³¹

Striped bass can be found along the East Coast of the Atlantic Ocean from northern Florida to the maritime providences of Canada. However, spawning occurs in only a few areas, with the Hudson River and Chesapeake Bay accounting for nearly all stocks. During times of peak abundance, fish spawned in Chesapeake Bay may contribute as much as 90% of the coastal migratory stocks.¹⁷

Striped bass are voracious predators and as a result grow rapidly. In their second year of life they are already pan-sized fish. In the first few years of life stripers tend to be pelagic schooling fish and are found pursuing forage fish in the open waters of Chesapeake Bay. As they grow older they tend to be more solitary. Striped bass can live as long as 30 years, but most fish are caught at less than eight years old.^{131,138}

Prior to the closure of the Maryland fishery on January 1, 1985, striped bass were the most sought after commercial and recreational finfish in the Maryland portion of Chesapeake Bay.¹¹¹ Striped bass stocks began an alarming long-term decline in abundance in the mid-1970's, due primarily to overfishing. The 1985 striped bass moratorium has allowed the spawning stock to recover to the extent that Maryland briefly reopened the commercial and recreational fishery in 1990 and 1991. Some 78,000 recreational

fishermen caught so many striped bass in one weekend in the fall of 1990 that Maryland closed the fishery after only ten days; even so recreational fishermen caught 130% of their quota.²⁰⁴

There is increasing concern that low DO in the deeper waters of the upper Chesapeake Bay and its tributaries has eliminated much of the summer habitat of subadult and adult striped bass. Optimum water temperatures for adult striped bass are 20-22°C; adults avoid waters > 25°C if cooler waters are available. Striped bass of all ages avoid water with DO < 3-4 mgL⁻¹. In 1984-1987 there was no suitable habitat (water temp. < 25°C and DO > 2 mgL⁻¹) remaining in late July in north-central segments of the Chesapeake Bay.⁴⁴

Similarly, the Broomes Island area of the Patuxent River is no longer acceptable summer habitat for striped bass. White perch, hogchokers, and striped bass dominated monthly trawl catches at Broomes Island from 1965-1968, but by 1988-1989 striped bass only rarely were caught there. Eutrophication and the resulting increase in hypoxic bottom waters is the probable cause of the deterioration of this summer habitat.²³⁷

BACKGROUND

Striped bass are the largest member of the family Percichthyidae, order Perciformes. Prior to 1966 they were placed in the sea bass family (Serranidae).

Striped bass have an elongated body which is moderately compressed. Their color ranges from light green to olive or steel blue, to brown to black. The sides of stripers are silver with seven to eight characteristic dark continuous stripes. One stripe always follows the lateral line and three stripes are always below the lateral line. The undersides of the fish range from white to silver with a brassy iridescence.^{69,171}

Literature reviews and synopses of striped bass include: Hildebrand and Schroeder,⁹⁴ Raney,¹⁹² Mansueti,¹³⁸ Hardy,⁸⁴ Westin and Rogers,²³⁶ Setzler *et al.*,²⁰⁹ Public Service Electric and Gas,¹⁹⁰ Nicholson,¹⁷¹ and Atlantic States Marine Fisheries Commission (ASMFC).⁶

Distribution

Striped bass range from the St. Lawrence River in Canada to the St. Johns River on Florida's east coast and from the Suwannee River in western Florida to Lake Pontchartrain, Louisiana. Striped bass were introduced into the San Francisco Bay Delta in 1879 and 1881; today they range from the Columbia River south to Ensenada, Mexico.⁸⁴ The principal spawning and nursery areas of striped bass along the Atlantic Coast are the Chesapeake Bay and its tributaries,¹⁵⁶ and secondarily the Hudson and Roanoke Rivers.^{3,6}

Migrations

The migratory behavior of coastal striped bass is more complex than that of most other anadromous species with seasonal movement and location of the fish related to age, sex, degree of maturity, and natal river (Map Appendix). In addition, there is considerable variation in the migratory behavior of fish of the same age, sex, and degree of maturity. Despite these differences, certain behavior patterns are common to most stocks. Generally sexually immature fish of both sexes remain in their natal estuary until about age II. After age II, the majority of females and some males leave the estuary and undertake seasonal coastal migrations.

The migratory behavior of Chesapeake Bay stocks of striped bass is a topic of continuing research. It is generally thought that approximately half of immature age III females migrate from Chesapeake Bay to coastal waters. Lesser proportions of age II and age IV females also leave the Bay. These females form the basis of the Atlantic coastal migratory population which moves northward along the coast in early spring, summers from Long Island north to the New England coast and the Maritime Provinces of Canada, and in the fall migrates southward and overwinters in coastal waters from New Jersey to North Carolina. Large numbers of striped bass, but not necessarily those fish that have spent the fall in coastal waters, overwinter in deeper water of the Chesapeake Bay and its tributaries.¹²⁰ Sexually mature fish begin migration to their spawning locations in early spring and return to coastal waters after spawning.⁶

Striped bass overwintering in Maryland waters of the Chesapeake Bay typically are smaller than 22 inches (559 mm) total length (TL). Fish overwintering in tributaries tend to be smaller than fish overwintering in the main stem of the Bay.^{143,144,145,146} Coastal tagging studies suggest that immature females that join the migratory stock do not return to their natal waters until they are sexually mature and participate in the spring spawning migrations.¹²⁰

The 1985 Maryland striped bass moratorium and strict conservation measures adopted by ASMFC have allowed a complete reassessment of age-specific migration rates from Chesapeake Bay without the confounding effects of fishing exploitation. Surveys conducted by the Maryland Department of Natural Resources (MDNR) in the upper Bay and the Choptank River during the fall and winter, when only resident pre-migratory fish are present, indicate the following migration rates from the Bay: 0% of age I, 10% of age II (both males and females), and 42.5% of the remaining ages III-VIII (50% of females and 35% of males). Extrapolating from these figures, one would expect the resident, premigratory Chesapeake stock to include approximately 25% (male) and 11% (female) of age VI striped bass, 16% (male) and 6% (female) of age VII, and 10% (male) and 3% (female) of age VIII.²⁰³

Chesapeake Bay fish have the widest range of movements in coastal waters of all the migratory striped bass stocks. Chesapeake Bay striped bass were captured in the Kouchibouguac River, New Brunswick (near the mouth of the St. Lawrence River).^{97,98,191}

The relative contribution of a stock to the coastal fishery depends upon the sex of the fish and the relative year class strengths of the contributing stocks. In the mid- 1970's, during times of peak abundance, Chesapeake Bay stocks of striped bass, primarily females, comprised approximately 90% of the Atlantic coastal migratory population.¹⁷ Studies in the early 1980's, a time of depressed Chesapeake Bay stocks, indicated that from one-half to two-thirds of the Rhode Island catch originated in Chesapeake Bay. The remaining striped bass were of Hudson River origin.^{60,172}

Chesapeake Bay Subpopulation

Researchers have used a variety of methods to identify subpopulations of striped bass in the Chesapeake Bay. Some early studies relied on meristic counts to separate striped bass from the James, York, and Rappahannock Rivers and the upper Bay into subpopulations. Others used morphometric analysis to identify subpopulations of striped bass in the four major Western Shore tributaries.^{127,133,170,193} The upper Bay stock has been more finely divided into Elk River, Choptank River, and Nanticoke River subpopulations with electrophoretic techniques.¹⁶⁴ However, Sidell *et al.*²¹⁶ were unable to separate upper Bay stocks of striped bass by protein electrophoresis.

Seventy percent of young-of-year striped bass from the Potomac, Patuxent, Choptank, and Nanticoke Rivers were correctly assigned to their natal rivers by analysis of the elemental composition of otoliths. Classification was increased to nearly 90% when data from the Choptank and Nanticoke were combined to form an Eastern Shore group, and data from the Potomac and Patuxent were combined to form a Western Shore group.¹⁶⁹

Recent surveys of mitochondrial DNA (mtDNA) variation provide evidence of distinct spawning aggregations in the Rappahannock, Potomac, Choptank, and upper Bay areas. These studies also suggest higher female than male fidelity to natal regions.^{33,34} The mtDNA variation in striped bass from the 1982 year class was examined in fish caught between 1984 and 1987. By examining mtDNA genotypes in male striped bass and mtDNA haplotype frequencies in females, Chapman³⁴ reached these conclusions: (1) distinct matriarchal groups occupied spawning grounds in the Choptank, Potomac, and upper Bay; (2) following the second year of life, mixed aggregations of males and females formed over the winter, probably derived from populations not surveyed in 1984; (3) males from these mixed aggregations appear to have dispersed

randomly to spawn in 1986, which suggests that males do not have a strong homing instinct; and (4) females appear to return to their natal areas, as their mtDNA frequencies in 1987 closely matched 1984 distributions (this conclusion assumes that striped bass tend to remain in their natal areas until age II.)

Earlier tagging studies conducted in the Chesapeake Bay support these conclusions. They suggest that larger males (ages III-IV) move greater distances within the Bay than smaller males (young-of-year and age II).^{138,147} Striped bass from the James and York Rivers also tend to migrate northward into the Bay proper.¹⁴⁷

Recruitment and the Maryland Juvenile Seining Index

The only available measure of recruitment of upper Bay striped bass into the fishable population is the Maryland juvenile seining index (JI; Table 1). This index is based on the average catch of young-of-year striped bass per seine haul at 22 permanent stations in four major spawning areas in Maryland waters of the Bay and its tidal tributaries. Begun in 1954, it is the only juvenile index of Atlantic anadromous stocks which has correlated significantly with subsequent commercial landings.^{9,39,63,186,206} The JI two to five years prior to the year of commercial landings explained 83% of the variation in Maryland landings during the period 1963-1983.⁷⁰ From 1973 through 1983 when the commercial fishery caught primarily younger striped bass, 84% of the variation in landings could be attributed to the JI two and three years prior to the commercial landings, which indicated increased fishing mortality during this time.⁷⁰

The ASMFC adopted the Maryland JI as part of its Interstate Striped Bass Fisheries Management Plan. Amendment 3 to the ASMFC Plan required the states to "reduce fishing mortality on the 1982 year class females, and females of all subsequent year classes, by 95% until the females of these year classes have an opportunity to reproduce at least once." This objective was intended to apply to the fishery until the 3-year running average of the Maryland JI attained 8.0,⁴⁰ which would approximate historical levels of recruitment.

Virginia Seining and Trawl Surveys

The juvenile abundance index for Virginia waters of the Bay is a pooled geometric mean of beach seine surveys conducted during the summer in the three major Virginia spawning areas: the James, York, (including stations on the Pamunkey and Mattaponi) and Rappahannock Rivers. The survey was conducted from 1967-1973, discontinued for seven years, and resumed in 1980. The Virginia seining index has increased steadily since 1981 and reached its highest value (15.8 striped bass per haul) in 1987.¹⁹¹

Virginia also began a generalized trawl survey in 1955 designed to monitor many fish and invertebrate species.⁴⁰ The gap in the seine survey coupled with recent fishing restrictions makes it impossible to correlate the Virginia seining index with commercial landings. But Virginia's annual trawling and seining indices are positively correlated ($P = 0.004$; $r^2 = 0.57$). Correlating the trawl survey with commercial landings has produced mixed results, with no relationship in the York River, but a strong relationship in the Rappahannock River, where a sharp peak in the juvenile index in 1970 was followed by a peak in commercial landings four years later.⁴⁰

LIFE HISTORY

Spawning

Striped bass spawn in the Chesapeake Bay area from early to mid-April through to the end of May, primarily in tidal freshwater areas just above the salt wedge. Major spawning areas (Map Appendix) include the James, Pamunkey, Mattaponi, Rappahannock, Patuxent, and Potomac Rivers on the Western Shore; the head of the Bay with the Susquehanna Flats, Elk River, Chesapeake and Delaware (C & D) Canal; and the Choptank and Nanticoke Rivers on the Eastern Shore,¹³⁹ (personal communication: Harley Speir, MDNR, 1987).

Spawning activity apparently is triggered by a rise in water temperatures. Throughout their range, striped bass spawn at water temperatures ranging from 11-24°C; peak spawning in the Chesapeake Bay area occurs at water temperatures of 14-19°C²⁰⁹ (Table 2). Spawning times may vary from year to year due to annual temperature variations. In Chesapeake Bay, one to three peaks occur during each spawning season with the major peak occurring any time from mid-April through the first weeks of May.^{102,174,211,228}

Incubation and Hatching

Striped bass eggs hatch from 29 (22°C) to 80 h (11°C) after fertilization. The relationship between incubation time and temperature is:

$$I = -4.60 T + 131.6;$$

where I is incubation time in hours and T is temperature (°C).¹⁸⁷

At hatching, striped bass larvae range from 2.0-3.7 mm TL and average 3.1 mm. The mouth has not yet formed (the mouth forms in 2-4 days) and the eyes are unpigmented. Eye pigmentation occurs around 5 mm TL. Nourishment is derived from a very large, initially oval yolk mass with a large oil globule projecting beyond the head, or at least anterior to the eyes.⁸⁴ Striped bass larvae retain yolk material and the oil globule much longer than other *Morone* spp.; traces of oil usually can be found in the livers of larvae less than 10 mm TL.

Eggs produced by striped bass females weighing 10 pounds (4.5 kg) or more are larger, have greater amounts of yolk and oil reserve, and have a greater probability of hatching than eggs produced by females weighing less than 10 pounds.²⁴⁴ Striped bass spawned from these larger females are larger at five days posthatch than larvae spawned from smaller females. These larger larvae with their greater food reserves may be able to withstand food deprivation for a longer period of time than larvae hatched from smaller eggs. Thus, the age structure of a striped bass stock may affect not only its population fecundity but also its viable egg production.^{58,197,199,244}

The percentage of viable eggs does not track year-class success as indicated by Maryland's JI. Thus the annual percentage of viable eggs collected in the Nanticoke estuary from 1962-1980 ranged from 11.6% in 1969, a year of average recruitment, to 75.7% in 1977, a year of poor recruitment. No declining trend in the viability of striped bass eggs is apparent in the upper Bay.¹⁴³

Larvae

Typically striped bass larvae begin feeding about five days after hatching at a size of ~5 mm TL, depending on water temperature.²⁰⁹ Temperature also affects the one month approximate duration of the larval stage.

Growth rates of ten otolith-aged cohorts of larvae from the Potomac River in 1987 averaged 0.28 mm d⁻¹ and ranged from 0.18-0.43 mm d⁻¹. Variability in growth rates among cohorts makes it impossible to differentiate all spawning cohorts from larval length-frequency distributions, especially over a protracted spawning season. Predicted lengths of striped bass larvae at 30 days post-hatch from cohort-specific regressions ranged from 10.6-15.4 mm standard length (SL); predicted ages of 15.0 mm larvae ranged from 29-55 days post-hatch.¹⁰³

A study of Choptank River larvae from 1980-85 found instantaneous growth rates (derived from increases in weekly mean lengths) ranged from 0.31 (0.56 mm d⁻¹) in 1985, to 0.21 and 0.22 (0.37-0.40 mm d⁻¹) in 1981 and 1980, respectively²²⁸ (see **Water Quality** for a discussion of the impact of light and turbidity on feeding and growth rates). The Choptank River studies showed that year-class success, as measured by the JI, is established by the late larval or early juvenile stage, and is correlated with minimum water temperature during the peak spawning period, and rainfall during the early postlarval period:

$$JI = 2.78T - 2.07R - 27.8;$$

$$r^2 = 0.95, p < 0.01, df = 4; \text{ where } T \text{ is temperature } (^{\circ}\text{C}) \text{ and } R \text{ is rainfall (cm).}^{228}$$

Survival of striped bass larvae depends primarily upon events during the first three weeks of life.²²⁸ The relative yearly abundance of striped bass larvae from 10-23 mm is

significantly correlated to the Choptank JI ($P < 0.05$); and the catch of striped bass larvae and early juveniles during the last week of May and first week of June is correlated strongly with the Choptank JI ($P < 0.003$).

As striped bass larvae grow, they are found progressively deeper in the water column. During the day, greatest densities are found near the bottom; larval densities from both mid-depth and bottom samples were significantly greater than densities from surface samples.¹⁶² Greatest densities of 8-12 mm striped bass larvae were at mid-depth during daylight hours; greatest densities of larger larvae tended toward the bottom.¹⁰²

Instantaneous daily mortality (Z) rates of 12 striped bass larval cohorts identified in the Potomac River in 1987 ranged from 0.048-0.917. Mortality rates of eight cohorts observed on three or more weekly sampling cruises averaged 0.197 (19.9% d⁻¹) and ranged from Z = 0.082 to Z = 0.388. No striped bass hatched prior to April 24 survived to 15 or 20 days post-hatch age.¹⁰³

Most potential striped bass recruits from the 1987 spawning season on the Potomac (larvae 20 days or older) were hatched from April 24th through May 17th. None of the cohorts dominated potential recruitment, although the April 27-29 cohort was most abundant in Tucker trawl catches in early June.¹⁰³

Daily losses of 6-12 mm TL striped bass larvae in the Choptank River ranged from 5.4% d⁻¹ in 1985 (Z = 0.055) to 19.3% d⁻¹ (Z = 0.222) in 1980.²²⁸ Although there is a propensity for episodic mortalities during early life history stages, the major controls on larval abundance and eventual recruitment may result from subtle among-cohort differences in daily growth or mortality rates. Small changes in growth or mortality rates of only 5% d⁻¹ can generate order-of-magnitude differences in expected cohort survival at metamorphosis. The variability in Z (daily instantaneous mortality rate) seems especially important for striped bass.^{10,100,101,103}

Juveniles

Striped bass larvae begin metamorphosis to the juvenile stage at ~20 mm; 17-20 mm larvae move inshore and spend the summer and early fall in shoal waters less than six feet (1.8 m) deep.²¹¹ In the Potomac River young-of-year striped bass begin this shoreward movement by early June. As juveniles grow, they move progressively down-river into low salinity waters.^{22,53,211}

In a two-year study in the Potomac River more striped bass juveniles were caught by beach seine than in otter trawls or bottom sleds.^{25,211} Juveniles caught in beach seines had greater feeding success (more food by weight in stomachs of individual fish) than those caught in the trawl and

bottom sled samples. Shallow-water, nearshore areas seem to be preferred habitats of juvenile striped bass.^{22,24}

Growth rates of young-of-year striped bass from the Potomac River averaged 0.7 mm d⁻¹ in 1975 and 0.6 mm d⁻¹ in 1976.²¹¹ Abundances of subadult striped bass have been, at times, sufficient to depress growth rates. Two-year old striped bass caught in the Patuxent River from July to November in 1960 did not increase in average size. Shearer *et al.*²¹⁵ concluded that this observation was evidence of density-dependent growth.

Sexual Maturation

Sexual maturation of striped bass appears related to latitude or ambient temperatures: fish from southern waters generally mature at an earlier age than those from regions to the north. In the Chesapeake Bay region, most males are sexually mature by ages II or III.¹¹¹ Typically only sexually mature fish participate in upriver spawning migrations.

Although studies conducted in the 1970's suggested earlier sexual maturity by females,¹¹¹ more recent intensive spawning stock studies conducted in Maryland waters suggest that very few females are sexually mature at age III (less than 500 mm TL) and that only a small percentage of age IV females (> ~500 mm TL) return to spawn. Complete recruitment to the spawning stock may not occur until ages VII or VIII.^{145,146}

Fecundity of striped bass is strongly related to fish size and, thus, age. Westin and Rogers²³⁶ summarized relationships between gonad weight, egg number, body length, and body weight among striped bass of various ages from Atlantic coastal populations. Goodyear⁷¹ developed a quantitative relationship between fish size and fecundity for use in population modeling.

Adults

Growth rates and average lengths of both male and female striped bass from various populations were summarized by Setzler *et al.*²⁰⁹ After age IV, female striped bass from Chesapeake Bay were larger than males.¹³⁸ Through age III annual increments of Chesapeake Bay striped bass were about 120 mm; between ages IV and VII annual growth increments were ~60-70 mm; and after age VIII annual increments were generally about 50 mm.¹³⁸

Female striped bass live longer than males; most fish age XI and older are females.²⁰⁹ Large striped bass, which may weigh as much as 125 pounds (46.6 kg), are almost exclusively females; the largest male striped bass reported either in Hudson River or Maryland waters was 110 cm (17 kg).⁶

Mortality estimates of various striped bass populations were discussed and summarized by ASMFC.⁶ Although an

annual natural mortality of about 15% has been assumed in numerous modeling studies (e.g., Polgar¹⁸⁶), the only estimates of natural mortality derived from field data are from Chadwick.³² His values range from 15-30% and were established for a number of different ages of California stocks.

Estimates of fishing mortality on striped bass populations vary widely, from about 20% to over 90%.⁶

ECOLOGICAL ROLE

Principal Foods

Striped bass larvae begin feeding at approximately five days post-hatch, at about 5.0 mm TL. Larvae feed primarily on copepodite and adult stages of copepods and cladocerans. The calanoid copepod *Eurytemora affinis* is a major prey in April. Major foods in late May and early June are the copepods *Acartia tonsa* and *Cyclops* spp., and the cladocerans, *Bosmina longirostris* and *Daphnia* spp.^{212,228} Striped bass larvae and early juveniles reared in freshwater ponds feed on cladocerans, adult copepods, and chironomid larvae.⁶²

Results from laboratory experiments demonstrate that striped bass larvae can forage and grow well [instantaneous growth rate (G) = 0.143 to 0.179 d⁻¹ (0.30-0.40 mm d⁻¹)] at food concentrations ranging from 50-250 individuals L⁻¹ of the copepod, *Eurytemora affinis*. Copepods were stocked to maintain a 70% nauplii and a 30% copepodite and adult ratio, which approximates the ratio of their life stages in nature.³⁷ Such zooplankton densities (either copepods or combined copepods and cladocerans) are typically encountered in Chesapeake Bay spawning areas when striped bass larvae are abundant.^{211,228} Thus, for example, Uphoff²²⁸ reported that zooplankton prey densities in the Choptank River averaged 71 L⁻¹, 96 L⁻¹, and 288 L⁻¹ during the 1983, 1984, and 1985 spawning seasons, respectively. Copepods constituted 58%, 53%, and 99% of the prey organisms during these three years; the remainder were cladocerans.

Juvenile striped bass (25-100 mm) are non-selective and flexible in their feeding habits. They consume insect larvae, polychaetes, larval fish, mysids, and amphipods. Oligochaetes and insects were the most abundant prey of juvenile striped bass in freshwater portions of the Potomac Estuary, whereas amphipods, mysids, fish larvae, and to a lesser extent, polychaetes and mollusks were more important in the higher salinity areas.²⁴ Fish become increasingly more important in the diets of juvenile striped bass larger than 100 mm, and by age II striped bass are primarily piscivorous.¹²

Adult striped bass in the Bay are piscivorous. Fish comprised 95.5% by weight of the total diet of adult fish.⁹⁹ Changes in striped bass diet reflected seasonal variations

in Bay fish populations. During the summer and fall bay anchovy and Atlantic menhaden were the dominant prey; by winter larval and juvenile spot and Atlantic croaker, which use the Bay as winter nursery areas, dominated the diet. White perch were the most prevalent prey consumed in the early spring, and alewife and blueback herring were the most abundant prey in late spring and early summer.⁹⁹

Predation

The relative importance of starvation and predation as major causes of mortality of larval fishes has initiated much debate and research in recent years.^{10,100,107,224} After reviewing the literature, Houde¹⁰⁰ concluded that predation may be the major cause of larval mortality for species with relatively robust larvae like striped bass. There is increasing consensus^{10,107,108} that predation typically is the primary contributor to mortality during egg and larval stages of teleosts. The ability of fish larvae to avoid predation depends upon both the size⁶⁴ and the age³⁰ of the larvae.

Juvenile white perch are potential predators of striped bass larvae,^{163,209} as indicated by their consumption of large numbers of striped bass larvae in laboratory experiments. Although their consumption of striped eggs was relatively low, their predation rate on larvae ages seven to 12 days post-hatch (DPH) increased to about 15 larvae per 15 minutes. Predation rates declined on larvae larger than 10 mm SL and 1600 μ g dry weight. Most striped bass were no longer vulnerable to predation at 42-54 DPH. Predation rates on eggs and larvae did not differ significantly between large and small females. Larvae were less vulnerable to predation in darkness than in light. Increased turbidity, however, resulted in increased rates of predation on yolk-sac larvae.¹⁶³

Laboratory trials¹⁵⁰ indicated juveniles or adults of the following species, common in striped bass spawning areas in the Bay, fed on yolk-sac larvae: spottail shiner, satinfin shiner, bluegill, pumpkinseed, tessellated darter, white perch, channel catfish, and white catfish. Consumption of yolk-sac larvae by shiners increased as the prey density increased to a maximum density of 3300 yolk-sac larvae per m^3 . Predation rates by satinfin and spottail shiners reached maximums of 81 and 150 larvae per predator per hour, respectively. At ambient densities of striped bass larvae found in the Pamunkey River (20-100 larvae per m^3), consumption by spottail and satinfin shiner ranged from 0-100%.¹⁵⁰

There is limited evidence of predation on striped bass yolk-sac larvae (prolarvae) by predatory copepods. The predatory copepod *Cyclops bicuspidatus thomasi* was found attached to both larval striped bass and white perch in the Chesapeake and Delaware Canal. However, this may have been an artifact caused by retention of both fish larvae and copepods in the collection gear for several

minutes. The cyclopoid copepod, *Acanthocyclops vernalis*, attached to and killed striped bass yolk-sac larvae when both species were placed in laboratory aquariums.¹⁵⁰

It is extremely difficult, if not impossible, to demonstrate conclusively predation on striped bass larvae in field studies. It is difficult enough to differentiate between striped bass and white perch larvae in preserved samples, let alone attempt to identify partially digested *Morone* larvae in a predator's stomach. Immunological techniques might be useful in producing evidence of predation on larval striped bass.

Starvation

Striped bass larvae have been found in poor nutritional condition in major nursery areas of the Bay. The majority of striped bass larvae caught in the Potomac estuary during 1981 and in the Choptank estuary during 1983 and 1984 were in poor nutritional condition according to studies by histological and morphometric techniques.²¹⁴ Results of fatty acid analyses from laboratory studies^{140,141} and field studies²¹⁴ indicated that first-feeding striped bass larvae were susceptible to starvation; older (larger) larvae were more resistant to starvation. The poor condition of striped bass or any other fish larvae certainly adversely affects their chances for survival, whether they succumb directly to starvation or whether the decreased growth rates of starved larvae make them more vulnerable to predation, disease, and poor water quality.

HABITAT REQUIREMENTS

Water Quality

Table 2 summarizes water quality conditions favorable to the survival of striped bass eggs, larvae, and juveniles, the most sensitive life stages of striped bass. Although survival in these early stages may occur outside some of the limits in Table 2, such conditions could be stressful. A discussion of suitable water quality parameters and stressful conditions for both striped larvae and juveniles follows.

Dissolved Oxygen

Dissolved oxygen concentrations $> 5 \text{ mgL}^{-1}$ are recommended for all life stages of striped bass¹⁸ (Table 2). Although Harrell and Bayless⁸⁵ reported that striped bass eggs could hatch at 3 mgL^{-1} DO at approximately 19°C , Turner and Farley²²⁵ found that $\text{DO} \leq 4 \text{ mgL}^{-1}$ caused deformities and reduced the hatch of striped bass eggs at $\sim 18^\circ\text{C}$. Other authors conclude that DO of at least $4.9\text{-}5.0 \text{ mgL}^{-1}$ (18°C) is required for normal hatching.¹⁷⁵

Suitable DO for striped bass larvae and juveniles is $5\text{-}6 \text{ mgL}^{-1}$ (Table 2). Yolk-sac larvae do not survive at 2.4 mgL^{-1} DO at 18°C .²⁰¹ Mortality of juvenile striped bass occurs at $\text{DO} < 3.0 \text{ mgL}^{-1}$; ^{38,42,124} $\text{DO} > 3.6 \text{ mgL}^{-1}$ is required for survival of juvenile striped bass.²³ Low DO adversely

affects appetite.⁹⁵ Juvenile striped bass acclimated at 18°C generally avoid DO of 3.8–4.0 mgL⁻¹ (41–44% of saturation) in experimental gradients.¹⁵⁵

With one exception, striped bass were collected in the Patuxent River only from locations with DO ≥ 6 mgL⁻¹ during the 1988–89 intensive trawl survey. Likewise, most striped bass caught in the Choptank River and the Upper Bay during this trawl survey occurred at DO of ~ 6 mgL⁻¹ or greater.²⁰² Striped bass of all ages avoid waters with DO < 3 –4 mgL⁻¹.^{35,42,202}

Salinity

Salinity stabilizes pH and provides osmotic balance. Low salinities apparently enhance survival of striped bass eggs,^{1,167} although most striped bass spawning in the Chesapeake Bay area occurs in tidal fresh water. A survey of 57 striped bass hatcheries in the United States indicated that salinity of 0.5 ppt or greater was the most important factor influencing survival.⁶⁶ Salinities from 2–10 ppt enhanced survival of eggs, larvae and juveniles in hatcheries.^{20,116}

Low salinity increases both growth and survival rates of striped bass larvae. Optimal salinities for growth and survival ranged from 3–7 ppt; larvae tolerated salinities from 0–15 ppt.¹ Several studies concluded that low salinities of 1.0–2.3 ppt are optimal for survival of striped bass larvae.^{11,68} Greater survival of larvae occurred at 8 ppt than in fresh water.²⁸ However, Bayless¹⁴ and Morgan *et al.*¹⁶⁸ concluded that salinities of 10–10.5 ppt were optimal for survival of larvae.

Most striped bass caught during the 1989 trawl survey occurred at salinities of 12–15 ppt (Patuxent), 3–9 ppt (Choptank), and 0–12 ppt (upper Bay).²⁰²

Suspended Solids and Turbidity

High concentrations of suspended solids (1000 mgL⁻¹) significantly reduced hatching of striped bass eggs⁸. Concentrations of 500 and 1000 mgL⁻¹ of suspended solids reduced the survival of striped bass larvae.⁸ Morgan *et al.*¹⁶⁸ reported a 48 h LD₅₀ of 3411 mgL⁻¹ of suspended solids (clay and silt).

Increased turbidity concentrations can adversely affect the ability of striped bass larvae to capture some types of zooplankton prey. When larvae were fed natural prey assemblages, primarily copepods, they consumed approximately 40% fewer prey in suspended solids concentrations of 200 and 500 mgL⁻¹ than in concentrations of 0 or 75 mgL⁻¹. In contrast, larvae fed the cladoceran, *Daphnia pulex*, captured the same average number of prey at all suspended solids concentrations tested.²⁶

Concentrations of suspended solids (sediment, detritus, and phytoplankton) reported in spawning areas of the

Bay and its tributaries range from less than 10 to several hundred mgL⁻¹. Suspended solids in the spawning reaches of the Choptank River during 1983 and 1984 (two wet years with greater than average streamflow) ranged from 8–522 mgL⁻¹.²⁶

Differences in the effects of turbidity on the susceptibility of copepods and cladocerans to predation may be important in nursery areas.²⁶ Changes in the nutritional condition of striped bass larvae in the Potomac estuary paralleled changes in densities of cladocerans, even though combined densities of copepods and cladocerans were relatively constant.¹⁴² High turbidity may contribute to larval starvation or poor condition in spawning areas where copepods are abundant but cladocerans are scarce. High turbidity may have a less adverse impact in areas where cladoceran prey are abundant.²⁶

Light

Laboratory studies of growth and survival at variable conditions of light, food level, and turbidity have shown that light is the most important variable affecting ability of striped bass larvae to feed and grow.³⁷ Some striped bass larvae grew and survived under all conditions tested, including low light (0.4 lux), turbid-turbulent conditions, and complete darkness. Turbidity, light intensity, and turbulence all significantly affected the growth of striped bass larvae over the first 25 days post-hatch, but none of these factors had a significant effect on survival rate at a food concentration of 100 *E. affinis* L⁻¹. Instantaneous growth coefficients varied five-fold, ranging from a low of 0.021 d⁻¹ at 0.4 lux to 0.103 d⁻¹ in the 450 lux, 150 mgL⁻¹ kaolin turbidity treatment. Growth rates of individual larvae also varied five- to six-fold in these controlled laboratory experiments.³⁷

Temperature

Temperatures $\leq 12^\circ\text{C}$ are considered lethal to striped bass eggs and larvae⁴⁸ and have been a suspected cause of high mortalities of eggs, yolk-sac larvae (prolarvae) and early postlarvae in the upper Bay,¹¹⁷ the Potomac River,^{80,81,103} the Choptank River²²⁸ and elsewhere.^{21,53,132} Lethal low water temperatures resulted in a 65% loss of striped bass egg production in the Potomac River in 1987.¹⁰³ A drop in water temperature from 17.0 to 11.3°C within 36 h killed almost all yolk-sac larvae in the Chesapeake and Delaware (C&D) Canal in late April, 1976, several days after the onset of peak spawning activity.¹¹⁷ Striped bass year-class success on the Choptank River during 1980–1985 was significantly related to minimum water temperatures during peak spawning periods. Low water temperatures (11–12°C) reduced survival of both eggs and yolk sac larvae.²²⁸

Laboratory studies indicate that water temperatures < 11 – 12°C ^{166,167,198,200} and $> 23^\circ\text{C}$ ⁵⁵ to 27°C ¹⁶⁶ are lethal to striped bass eggs. Eggs and larvae from the C&D Canal in

Maryland and the Brookneal Hatchery in Virginia reared at 12°C had lower egg hatchability and poularvae survival and growth than those reared at 14-20°C.¹⁶⁷

Optimal temperatures for larvae range from 18-21°C,²⁰⁰ although larvae can tolerate water temperatures from 12-23°C.⁵⁵ Larvae are stressed at temperatures of 10°C;¹¹³ upper lethal limits (48 h LC₅₀) range from 28.9-32.8°C.¹¹⁴

Maximum growth rates of one-year old striped bass juveniles occurred at temperatures of 24-26°C.⁴⁷ Growth rates remained high (about 93% and 81% of maximum) for juveniles reared at 23.5 and 28°C, but dropped sharply to 50% of maximum at temperatures above 30°C.¹⁴⁸ Juvenile striped bass select temperatures near 25°C,¹⁵⁴ or 26°C⁴⁶ in thermal gradient studies. Acute (short-term) preferred temperatures of Hudson River juveniles were 29-31, 26-27, 23-24, and 14-17°C for acclimation temperatures of 24, 21-22, 17, and 6°C, respectively.²²²

The physiologically optimum temperature range for striped bass shifts to lower temperatures as the fish grow: for first year juveniles it is near 26°C,⁴⁶ whereas it is near 20-24°C for juveniles in their second year⁴⁵ and 20-22°C for adults.²⁰⁷ Older juveniles and adults avoid temperatures above 25°C when cooler water is available.⁴⁴

pH

A pH range of 7.0-9.5 is recommended for striped bass culture.^{20,116} Water from productive striped bass hatcheries surveyed by Parker¹⁸³ had slightly basic water (mean pH 7.3) whereas waters from less productive hatcheries were acidic (mean pH 6.4).

Striped bass larvae are adversely affected by even slightly acidic pH levels; pH < 6.0 is lethal to larvae.¹⁵¹ Eleven-day old striped bass larvae suffered 100% mortality after a two-day exposure to pH 5.5, and a seven-day exposure to pH 6.5 resulted in 89% mortality of 19-day old larvae.¹⁵² Salinity protects striped bass larvae against the toxic effects of low pH in laboratory experiments. In Chesapeake Bay the presence of salinity produces sufficient buffering capacity such that the pH of even slightly saline waters is neutral or slightly basic.^{210,213}

Slightly acidic pH also increases the mobilization of toxic metals such as aluminum. Thus, for example, 11-day old striped bass larvae suffered 21% mortality at pH 6.5. The addition of 200 µg/L⁻¹ aluminum at the same pH, however, resulted in 99% mortality.¹⁵¹

Poorly-buffered Eastern Shore tributaries such as the Choptank and the Nanticoke Rivers are susceptible to episodic drops in pH especially during wet years. The pH of rainfall in the Chesapeake Bay area averages 4.0, with individual events as low as 3.0 (pH of "normal" rainfall is 5.0-5.4 due to naturally occurring organic acids and CO₂

in the atmosphere¹⁴³). It is likely that low pH, with or without the influence of aluminum,²⁷ can create toxic conditions in these rivers during the time of spring runoff: the beginning of the striped bass spawning season. Even during relatively dry springs pH on the spawning grounds in Eastern Shore tributaries may be marginal. Average pH for stations sampled in peak spawning areas during the dry spring of 1986 ranged from 6.00-6.60 in the Nanticoke River and from 6.23-6.86 in the Choptank River.^{210,213}

Juvenile striped bass are more resistant to acidic conditions than larvae. Exposure of juvenile striped bass to pH 5.5 for seven days resulted in no significant increase in mortality.¹⁵² However, juvenile striped bass died after a 24 h exposure to pH 5.3.²²¹

Hardness and Alkalinity

Striped bass larvae survive better in hard water than in soft water.⁶⁷ Hardness > 150 mg/L⁻¹ is recommended for culturing striped bass, and hardness < 25-30 mg/L⁻¹ can lead to significant mortality unless salt is added.^{20,116} Striped bass larvae suffered 80% mortality after four-day exposures to 34.6 mg/L⁻¹ CaCO₃.²⁸ Striped bass larvae reared in freshwater with less than 60 mg/L⁻¹ CaCO₃ for five days suffered greater than 90% mortality.²⁰⁵ Poularvae reared in Nanticoke River water with hardness ranging from 23-20 mg/L⁻¹ suffered high mortality.⁷⁹ Juvenile striped bass reared at 25-30 mg/L⁻¹ hardness suffered greater mortality than juveniles reared at 150-200 mg/L⁻¹ CaCO₃.⁸⁸

Water quality contributed to poor year-class success in the Choptank River, especially in 1983 and 1984. During the 1983 spawning season, hardness measurements in the Choptank River never exceeded 150 mg/L⁻¹; 80% were < 60 mg/L⁻¹ and 20% of the measurements were < 30 mg/L⁻¹. More than half of the 1984 water samples during the spawning season were < 60 mg/L⁻¹ hardness, whereas in 1985 there were no samples < 60 mg/L⁻¹.²²⁸

Alkalinities > 150 mg/L⁻¹ are recommended for intensive striped bass culture,¹¹⁶ and concentrations < 81 mg/L⁻¹ have been associated with poor hatchery production.¹⁸³ Alkalinities in the Choptank River during the 1983-1985 spawning seasons ranged from 10-37 mg/L⁻¹. This range is below the recommended culture value and is the level found in poorly producing hatcheries.²²⁸

Structural Habitat

Depth

Adult striped bass are found in a variety of inshore habitats such as sandy beaches, rocky shorelines, shallow water, deep trenches, bays, and rivers. During a recent intensive trawl survey striped bass were caught at depths of 3-21 m; the largest catches occurred at depths of 6-13 m in the Patuxent, 3-11 m in the Choptank, and 4.5-8 m in the upper Bay above the Bay Bridge.²⁰² In winter during the coldest weather, striped bass concentrate in waters > 9 m

deep where temperatures are somewhat warmer than those at the surface. During warmer periods the overwintering fish often move out of the deep waters in search of food.

Flow, Temperature, and Reproduction

Hatchability of striped bass eggs and survival of larvae to the juvenile stage is strongly affected by environmental variables. Both the velocity and flow of freshwater are apparently related to successful spawning.^{1,6,55,86,137,187} Colder than normal winter temperatures (December) and greater than normal riverflow during April were associated with dominant year classes of striped bass in the Potomac estuary.^{25,161,226} However, this relationship does not appear to hold for upper Chesapeake Bay (personal communication: Walter Boynton, Chesapeake Biological Laboratory). Climatic factors, specifically previous December temperatures, April temperatures and April river flow most significantly affected striped bass stocks in the Potomac River from 1929-1976; pollution variables were not significant.¹⁸⁸

SPECIAL PROBLEMS

Nine factors initially were hypothesized to explain population declines of striped bass in the Chesapeake and Roanoke stocks during the late 1970's and the early 1980's: (1) toxic contaminants, (2) starvation of larvae, (3) over-exploitation, (4) predation of larvae, (5) unfavorable climatic events, (6) changes in water use practices, (7) competition with other species for food and space; and poor water quality due to (8) agricultural runoff and (9) sewage treatment practices.^{191,227} Table 3 presents a simplified summary of the research results to date from the examination of these hypotheses.

Starvation and predation of larvae are discussed above (**Ecological Role**).

Overfishing

Excessive fishing mortality is thought to be the predominant cause of the coastwide decline of adult striped bass in the late 1970's and the early 1980's.^{6,110,143} Male striped bass of the dominant 1970 year-class were removed by the Potomac River fishery at a rate of 60-70% per year at ages III and IV.¹²⁰ The MDNR estimated a total annual mortality rate of 45.2% for age VI females of the 1970 year class and a rate as high as 92.7% for age V males of the same year class. Approximately 63% of available males and 58% of available females were harvested annually during 1982-1985 in the upper Bay.¹¹⁰ It is likely that fishing mortality increased during the 1970's beyond earlier levels, particularly for adult females which were exploited most heavily along the Atlantic Coast by the recreational hook and line fishery.⁶³ Both the numbers of recreational fishermen,¹⁵⁷ and their efficiency⁶³ increased during the 1970's. This increased fishing mortality resulted

in critically low numbers of females on three of the four major spawning areas (Potomac and Nanticoke Rivers, and upper Bay) in Maryland during 1985.¹⁴³

Historically, striped bass have been subjected both to growth overfishing (fishing too small a fish for optimum yield) and recruitment overfishing (not allowing enough fish to successfully spawn). Both commercial and recreational fisheries depend upon the occurrence of periodic dominant year classes to sustain population levels.⁶³ Dominant year classes in Maryland occurred in 1958, 1964, 1966, and 1970. The dominant year class in 1970 resulted in peak commercial landings in 1973 of 5.6 million pounds. Maryland commercial landings declined to 359,000 pounds (excluding the Potomac River) ten years later. This decreasing trend in landings was preceded by a constant decrease in the JI from 30.4 in 1970 to 1.4 in 1983. Commercial landings increased to 800,000 pounds in 1984 as a result of the partial recruitment of the 1982 year class to the fishery.¹⁴⁵

Peak Virginia harvests occurred in 1963, 1966, 1969, and 1973.²¹⁹ Virginia commercial landings also have declined precipitously in the last two decades. The commercial striped bass fishery in the James River was closed in 1976 because of kepone contamination.

Historically, both Maryland and Virginia experienced depressions in catches in the early to mid-1930's and in the mid-1950's.²¹⁹ Stock levels were so low by the early 1980's however, that Maryland issued a total moratorium on the catch, sale, or possession of striped bass in the State effective January 1, 1985.

In addition to the commercial fishery, substantial quantities of striped bass have been harvested annually in the recreational fishery. During the 1970's, for the entire Atlantic Coast, the recreational striped bass catch exceeded the commercial catch by as much as 4.7:1.⁴ Estimates of the recreational catch in Maryland range from twice the commercial catch in 1962 (9.3 million pounds)⁵⁹ and 1.2 times the commercial catch in 1976 (2.2 million pounds)²¹⁸, to 70% of the commercial catch in 1979 (657,000 pounds).²³⁸ The magnitude of the Virginia recreational harvest is unknown.

Rago *et al.*¹⁹¹ summarized the recent coastwide management strategy:

"In response to the decline in commercial harvest and the perceived decline in the production of juvenile striped bass in the late 1970's, the ASMFC prepared a coastwide management plan for the anadromous stocks of striped bass (Roanoke, Chesapeake, Delaware, and Hudson), along the Atlantic Coast as part of its Interstate Fishery Management Program.⁵ Congress passed legislation in 1984 and 1988 enabling Federal imposition of a mora-

torium on striped bass fishing in those states that fail to comply with the coastwide plan".¹⁹¹

A number of state regulations affecting striped bass fishing were imposed as a result of the ASMFC striped bass management plan. Additionally, Virginia imposed a total moratorium on the striped bass fishery on June 1, 1989. Because Virginia does not allow fishing for striped bass from December 1 through May 31, the Virginia moratorium essentially has been in effect since December 1, 1988.

The Scientific and Statistical (S&S) Committee of the ASMFC proposed a limited harvest of striped bass that would still permit the population to grow to fully restored status. This limited fishery would be implemented when Maryland's young-of-year recruitment (JI) reached a 3-year running average of 8.0. The S&S Committee recommended, and the ASMFC accepted, a transition instantaneous fishing mortality rate (F) of 0.25, which is the equivalent of about 18% of legal-sized fish being harvested annually. Additionally, about 18% of striped bass die annually from natural causes such as disease and predation.

Although annual reproductive success in Maryland was relatively low during the early moratorium years of 1985-1988, one of the largest year classes on record was produced in 1989 [JI = 25.2 (Table 1)]. As a result of this high reproductive success in the upper Bay, and especially in the Choptank River, the Maryland three-year running average JI exceeded the trigger value of 8.0, providing enough recovery for a limited recreational and commercial fishery in the Chesapeake Bay in 1990-91. There were over 250,000 recreational fishing trips in the Bay and its tributaries during Maryland's recreational season in October 1990. Fishing pressure was so great and projected catch rates were so high that the State had to close the recreational fishery after only 16 days. Even so, recreational catches exceeded the 318,750 pound quota by 95,000 pounds.²⁰⁴ The charter boat fishery estimated catch was 98,000 pounds, 87% of their allowable quota.

Commercial striped bass landings in Maryland were lower than anticipated. Reported commercial harvest in the Bay and its tributaries was 130,900 pounds: 41% of the allotted quota of 318,750 pounds. Commercial harvest in the Virginia portion of the Bay was larger, and exceeded the 211,000 pound quota by 53,000 pounds (25%) even though the Virginia commercial season was closed after only five days.

Recreational and charter boat catches in Virginia totaled 80,700 pounds. Combined commercial and recreational catches in the Potomac River exceeded allotted quotas by 10%. The reopened striped bass fisheries in the Bay and its tributaries harvested an estimated 1,332,000 pounds

during the limited 1990-91 season. Additionally, MDNR estimates an additional 181,526 pounds of striped bass in the Maryland portion of the Bay were lost due to the combined affects of by-catch and poaching mortality. Approximately half of this mortality was a result of the by-catch mortality in the Maryland 1990 white perch gill net fishery (assumes 47% mortality of striped bass caught in gill nets).²⁰⁴

Interim Stocking Program in Chesapeake Bay

Maryland, Virginia and the U.S. Fish and Wildlife Service are jointly conducting a program of artificial propagation to supplement the Chesapeake Bay spawning stock. Since 1985, 2.5 million striped bass have been stocked, primarily in the Patuxent and the Nanticoke Rivers and the upper Bay. Recovery of phase I fingerlings (stocked at a size of 35-50 mm TL) in the Patuxent River during 1988 was sufficient to evaluate in-river survival after stocking. Phase I juveniles suffered about a 2.4% daily mortality during the first 85 days after release and 95% of all fish stocked remained within 10 miles (16 km) upstream or downstream of stocking locations.¹⁹¹

Contaminants

Toxicity to Single Contaminants

Table 4 summarizes acute toxicity data for contaminants most likely to affect striped bass eggs, larvae, and juveniles in Chesapeake Bay. Although the egg stage is considered less sensitive than larvae or juveniles, it was included because contaminant exposure to the egg stage may ultimately affect other life stages. Data in Table 4 were primarily derived from laboratory toxicity studies.

Most of the toxicity studies conducted with striped bass eggs have evaluated effects of either biocides or metals. Ozone-produced oxidants (OPO) were more toxic to striped bass eggs in freshwater than in saltwater; 30 h LC₅₀ concentrations were 0.06 and 0.21 mgL⁻¹.⁷³ Toxicities of total residual chlorine (TRC) to striped bass eggs are similar, ranging from 46 h LC₅₀ of 0.02-0.22 mgL⁻¹ to 100% mortality after a 36 h exposure to 0.06 mgL⁻¹,⁷² and 77% mortality after a 40 h exposure to 0.01 mgL⁻¹.¹⁶⁰ Dechlorination significantly reduced the toxicity of TRC.⁷²

Cadmium, dieldrin, rotenone and tributyltin were most acutely toxic (96 h LC₅₀ ~ 0.001 mgL⁻¹) to striped bass larvae.^{105,106,185} The least toxic compounds (expressed as 96 h LC₅₀) were: selenate (13.20 mgL⁻¹), arsenate (18.69 mgL⁻¹), sulfate (250 mgL⁻¹), potassium permanganate (100 mgL⁻¹) and chloride (1000 mgL⁻¹).^{105,106,119}

Endrin, endosulfan, and DDT were the most acutely toxic organic compounds to juvenile striped bass (96 h LC₅₀ of 0.000094, 0.0001, and 0.00053 mgL⁻¹ respectively).¹²² Cadmium was the most toxic metal tested (LC₅₀ 0.002-0.075 mgL⁻¹, depending on hardness and salinity).^{106,179,243}

Toxicity to Contaminant Mixtures

Assessing the effects of contaminant mixtures on striped bass survival is a realistic approach because these life stages are often exposed to several contaminants simultaneously in the environment. Chemical mixtures may exhibit synergistic (greater than expected), additive (as expected) or antagonistic (less than expected) effects.

Burton *et al.*²⁹ evaluated the effects of bleached Kraft mill effluent (BKME) on striped bass eggs and prolarvae. No mortality attributable to BKME up to 20% by volume was reported in three separate egg studies with continuous exposure from the time of fertilization through hatch. However, BKME concentrations ranging from 8-20% by volume caused significant mortality of prolarvae after 72 h exposures.

The effects of an organic-inorganic chemical contaminant mixture were evaluated on percent fertilization, percent hatch and prolarval survival of striped bass.⁷⁷ All dilutions of the contaminant mixture were considered to be realistic for Chesapeake Bay striped bass spawning areas. Percent fertilization (24 h exposure) and percent hatch (48 h exposure) were not significantly affected by various dilutions of the contaminant mixture. The full strength contaminant mixture significantly reduced survival of striped bass prolarvae after 144 h of continuous exposure from the time of fertilization.

Mehrle *et al.*¹⁵³ exposed striped bass larvae to a mixture of organic and inorganic contaminants in fresh well water and 2 ppt saline water. This organic-inorganic mixture was selected to simulate contaminant conditions reported in Chesapeake Bay striped bass spawning areas. Larvae were most susceptible to the contaminant mixture in fresh water. Thirty-day exposures at two and four times the environmental concentration (2x and 4x) caused significant mortality. A contaminant mixture concentration of 4x caused significant mortality in 30 d at 2 ppt salinity. Ninety-day exposures at 2x and 4x caused significant mortality in 5 ppt salinity.

In situ (caged) and on-site laboratory experiments in Chesapeake Bay spawning areas have demonstrated that survival of early life stages of striped bass can be significantly reduced by low pH, soft fresh water, and heavy metals in the Nanticoke and Choptank Rivers and by contaminants and sudden decreases in water temperature in the Potomac River.

Water in the Nanticoke and Choptank Rivers was extremely toxic to striped bass prolarvae in 1984 and 1987, and in the Nanticoke in 1986, when experiments were not conducted in Choptank. Suspected causes of mortality included low pH, dissolved aluminum, and soft (poorly buffered) fresh water in 1984; low pH in 1986; and low

pH, soft water, and high concentrations of aluminum, cadmium, and copper in 1987.

Studies conducted in the Potomac River in 1986 demonstrated significant mortality of both prolarvae and juveniles.^{76,151} Poor survival of prolarvae was likely caused by inorganic contaminants such as monomeric aluminum (90 $\mu\text{g/L}$), cadmium (7 $\mu\text{g/L}$), and copper (72 $\mu\text{g/L}$), and by sudden decreases in temperature below 11°C. In a separate study, Wright²⁴² demonstrated that both copper and cadmium concentrations from tissues of striped bass larvae collected in the Potomac River in 1986 were approaching tissue concentrations found in larvae exposed to potentially toxic concentrations of these metals in the laboratory. Likewise in 1988, significant mortality of both prolarvae and juveniles in the Potomac was attributed to potentially toxic concentrations of cadmium, lead, and chlordane, along with sudden drops in water temperature.⁸⁰

Compounding factors in interpreting the results of many of these field toxicity studies have been the presence of fresh water with very low buffering capacity in the nursery areas of the Choptank and Nanticoke Rivers, drops in water temperature to 10°C during some portion of the experiments in the Potomac River during both 1986 and 1988, and temperature drops to 11°C in the Choptank River in 1987. Exposure of striped bass eggs and prolarvae to soft fresh water with even slightly acidic pH results in high mortalities.^{20,28,66,116,151}

Eutrophication

There is increasing concern that low DO in the deeper waters of the upper Bay has eliminated much of the summer habitat of subadult and adult striped bass.^{42,43,44,189}

As eutrophication of the upper Bay has intensified, the volume of deep residual cool water (roughly the area from Tilghman Island to Rock Hall and centered near Annapolis) with suitable DO for larger striped bass has diminished progressively. Summer resident adult and subadult striped bass thus are forced to occupy warmer temperatures or areas of lower DO with resulting physiological stress, which may impair their reproductive capacity.⁴⁴

The Broomes Island area of the Patuxent River is no longer acceptable summer habitat for striped bass and white perch.²³⁷ White perch, hogchokers, and striped bass dominated monthly trawl catches at Broomes Island from 1965-1968, but in the 1988-1989 monthly trawl survey striped bass and white perch were extremely rare. Dominant species during the 1988-1989 trawl survey were spot, bay anchovy, and weakfish. Spot and bay anchovy¹⁵ are pollution tolerant species. Spot, now the dominant species in the middle Patuxent estuary, is one of the most

tolerant species to low DO; during the 1988-1989 trawl survey spot were most abundant at DO > 1.5 mgL⁻¹.²⁰²

There has been a three-month phase shift in the seasonal species diversity cycle in the Broomes Island area during the last two decades. During 1965-1968 species diversity indices were lowest in January and highest in late June and early July both at Broomes Island and upriver at Benedict Bridge. By 1988-1989 the time of the lowest species diversity shifted from January to April and the highest diversity shifted from July to October at Broomes Island. Upriver at Benedict Bridge, although the seasonal cycle of species diversity did not change, there was a small but significant decrease in species diversity in the summer months²³⁷ (for further discussion of changes in the fish community in the Benedict area, see WHITE PERCH: **Special Problems**, this volume).

The Patuxent River has changed greatly in the last 50 years as a result of increasing nutrient inputs and eutrophication.⁵² Chlorophyll *a* concentrations in surface waters at Broomes Island increased from 30-40 µgL⁻¹ during May-July 1968 to 17-138 µgL⁻¹ in 1978. Dissolved oxygen in bottom waters in the vicinity of both Broomes Island and Benedict Bridge was much lower in 1977-79 than in 1936-40.⁹⁰ During July-September 1988, bottom DO < 2 mgL⁻¹ was found in depths as shallow as 4.2 m.²³⁷

Severe declines in submerged aquatic vegetation, caused by nutrient-driven planktonic and epiphyte shading,¹¹⁵ have resulted in changes in the near-shore habitat of juvenile striped bass. The lack of suitable cover in these shoal areas increases in the vulnerability of juvenile striped bass to predation, and may be a factor contributing to the decline of striped bass.¹⁸⁹

Global Warming

A recent paper predicts a major loss of habitat for striped bass in the Chesapeake Bay during the next century because of expected global warming. Coutant⁴³ examined changes in Atlantic coast distributions of striped bass resulting from a doubling of atmospheric carbon dioxide as predicted by two global climate models. According to both models, the doubling of atmospheric carbon dioxide would produce water temperatures above 25°C from early July through mid-September in the entire Chesapeake Bay.

The expanding anoxia in the deeper waters of the Bay over the past two decades^{173,189} also may be intensified by climatic warming. This scenario would probably force all large striped bass to migrate from the Bay into coastal waters during the summer months. On the positive side, however, conditions in the Bay during the remainder of the year might be more suitable for striped bass - closer to the thermal niche - than they are now and thus might promote higher annual striped bass production.⁴⁵

Diseases

Parasitic and microbial infections usually are not intense enough to cause mortality among wild populations of striped bass unless other stressors are present. Few studies have been conducted in the Bay to evaluate the effects of contaminant stress on the susceptibility of striped bass to disease. Exposure of juvenile striped bass to sublethal total residual chlorine concentrations of 0.05-0.23 mgL⁻¹ did not increase their susceptibility to infection with the bacterial pathogen *Vibrio anguillarum*.⁹³ Exposure of young-of-year striped bass to a mixture of arsenic, cadmium, copper, lead, and selenium at 4 and 10 times the average environmental concentrations of 1-3 µgL⁻¹ protected the fish from experimental infection with *Flexibacter columnaris*, the causal organism of columnaris disease. When tested singly, copper was the only metal that protected against infection; arsenic increased the susceptibility of striped bass to infection.¹³⁴

Opportunistic fish pathogens were 100-1000 times higher in striped bass from the Hudson River, a highly polluted habitat, than in striped bass from Long Island Sound. The high percentage of pathogens in the gut flora of striped bass from both estuarine and marine environments might predispose striped bass to bacterial epizootics especially in conjunction with other environmental stresses.¹³⁵

Infectious pancreatic necrosis virus (IPNV), a pathogen of Atlantic menhaden, has been isolated from moribund striped bass being reared in a hatchery on the Bay.²⁰⁸ The IPN virus did not cause increased mortality in experimentally infected striped bass, even when fish exposed to the virus were stressed by an abrupt change in temperature or pH.²³² Striped bass became transiently infected after waterborne exposure. Although young-of-year juveniles were resistant to waterborne exposure, they became chronic virus carriers following ingestion of IPNV-contaminated food,^{232,233} or inoculation with the virus.^{230,232} Most IPNV-inoculated fish produced circulating virus-neutralizing activity even though virus could still be isolated from their tissues.^{232,233} Adults did not transmit IPNV to their progeny.²³³

The IPN virus was not isolated from any of young-of-year or older striped bass from Chesapeake Bay assayed for the virus. However specific IPNV-neutralizing activity was present in 10% of 1 to 3-year old striped bass, and in one young-of-year striped bass caught during the winter of 1984-85 in the upper Bay.²³¹ The virus has been isolated from Atlantic menhaden, a major prey of striped bass in the Bay, and Wechsler *et al.*²³³ hypothesized that consumption of IPNV-infected menhaden resulted in the presence of the IPNV-neutralizing activity found in some striped bass from the Bay. The IPNV isolated from striped bass and menhaden are closely related to each other and to the salmonid isolate.²³⁰ Carrier striped bass can transmit IPNV to brook trout in the laboratory, and IPNV causes

epizootic mortalities in salmonids.¹⁴⁹ Because of the threat IPNV-carrier striped bass pose to salmonids, striped bass should be assayed for IPNV prior to introduction into IPNV-free areas.^{230,232}

RECOMMENDATIONS

Increase Dissolved Oxygen

Dissolved oxygen of at least 5 mgL⁻¹ is required for all life stages of striped bass. Increasing below-pycnocline DO concentrations in summer months to at least 5 mgL⁻¹ in the oligohaline (0.5-5 ppt salinity) and mesohaline (5.1-18 ppt) portions of the Bay will increase suitable summer habitat for striped bass.

Subadult and adult striped bass prefer summer water temperatures from 20-22°C and avoid water temperatures > 25°C. Increasing DO concentrations of the upper Bay's deep residual cool waters to > 5 mgL⁻¹ would restore these important summer habitats of adult and subadult striped bass.

Improve Water Quality in Spawning Areas

Water quality must be improved in spawning areas. Striped bass eggs and larvae are affected adversely by even slightly acidic pH. Suspected causes of mortality of striped bass prolarvae include low pH and high concentrations of aluminum, cadmium, and copper in the Choptank and Nanticoke Rivers, and aluminum, cadmium, copper, lead, and chlordane in the Potomac River.

Turbidity from runoff should be reduced in nursery areas. Striped bass larvae consumed ~40% fewer prey in suspended solids concentrations of 200 and 500 mgL⁻¹ than in concentrations of 0 or 75 mgL⁻¹. Suspended solid concentrations in the spawning reaches of the Choptank River during 1983 and 1984 ranged from 8-522 mgL⁻¹.

Determine Hatchery Contributions to Spawning Stocks

Preliminary results from re-captured tagged hatchery-reared fish indicate that ~9% of the mid-Bay spawning stock, ~8% of the commercial harvest, and ~30% of the Patuxent River recreational fishery are of hatchery origin (personal communication: Ben Florence, MDNR, June 1991). These hatchery-reared fish are not yet fully recruited to the Bay spawning population. The impact of hatchery-reared striped bass on the genetic variation of wild stocks must be determined.

Quantify Estimates of Young-of-Year Recruitment

Mark and recapture studies currently underway in the Patuxent River with tagged, hatchery-reared larvae will:

(1) provide growth and mortality rates of cohorts of both wild and hatchery larvae; (2) quantify success of young-of-year recruitment; and (3) determine hatchery contribution to young-of-year recruitment. This research needs to be expanded to other Bay spawning areas to quantify estimates of young-of-year recruitment (i.e., determine the true abundance of juvenile striped bass represented by the JI). Quantification is necessary for more effective management of Chesapeake Bay stocks of striped bass.

Protect Spawning Stocks

The limited reopening of the Maryland striped bass fishery provides an opportunity to observe the population effects of fishing under carefully controlled and monitored conditions. The cumulative impact of increased fishing mortalities on the Chesapeake Bay spawning stock must be evaluated. Although current fishing restrictions generally appear to be protective, the recently initiated May trophy striped bass fishery in the upper Bay targets older and larger successful spawners returning from their spawning migrations. Because the trophy fishery targets the most important component of the spawning stock, it should be evaluated carefully.

SUMMARY

Striped bass is an anadromous species found along the East Coast from northern Florida to the maritime provinces of Canada. Most of the coastal migratory stock originates in Chesapeake Bay. Prior to the 1985 moratorium, striped bass were the most sought after commercial and recreational finfish in the Maryland portion of the Chesapeake Bay. Overfishing was the major cause of the decline of striped bass stocks in the mid 1970's. The moratorium allowed the spawning stock to recover to the extent that a limited commercial and recreational fishery was allowed in the Bay in 1990-1991.

Striped bass concentrate in areas with DO of at least 6 mgL⁻¹. Subadult and adult striped bass prefer water temperatures of 20-22°C and avoid temperatures > 25°C if cooler waters with DO > 5mgL⁻¹ are available. Increased DO in the cooler, deeper waters of upper Chesapeake Bay would restore suitable summer habitat for adult and subadult striped bass.

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STRIPED BASS

Table 1. Maryland striped bass juvenile index. Young-of-year striped bass per seine haul by area and year (unpublished data: MDNR).

Year	Nanticoke River	Choptank River	Head of Bay	Potomac River	Yearly Average	Three-year average
1954	25.1	1.2	0.9	5.2	5.25	
1955	5.9	12.5	4.4	5.7	5.5	
1956	8.2	9.8	33.9	6.2	15.2	8.6
1957	1.3	2.1	5.4	2.5	3.9	7.9
1958	22.5	19.5	28.2	8.4	19.3	12.5
1959	1.8	0.1	1.9	1.6	1.4	7.9
1960	4.7	9.0	9.3	4.3	7.1	9.3
1961	1.5	6.0	22.1	25.8	17.0	8.5
1962	6.6	6.1	11.4	19.7	12.2	12.1
1963	4.1	5.4	6.1	1.1	4.0	11.0
1964	13.3	10.6	31.0	29.1	23.5	13.2
1965	21.6	9.5	2.2	3.4	7.4	11.6
1966	3.3	13.6	32.3	10.5	16.7	15.9
1967	4.1	5.3	17.4	1.9	7.8	10.6
1968	9.0	6.3	13.1	0.7	7.2	15.6
1969	6.2	4.8	26.6	0.2	10.5	8.5
1970	17.1	57.2	33.1	20.1	30.4	16.0
1971	2.0	6.3	23.7	8.5	11.8	17.6
1972	25.0	11.0	12.1	1.9	11.0	17.7
1973	1.1	1.0	24.7	2.1	8.9	10.6
1974	3.9	15.3	19.9	1.5	10.1	10.0
1975	5.2	4.7	7.6	7.8	6.7	8.6
1976	1.7	2.4	9.8	3.2	4.9	7.2
1977	1.0	1.2	12.1	1.9	4.8	5.5
1978	4.8	6.0	12.5	7.9	8.5	6.0
1979	0.9	2.8	8.3	2.2	4.0	5.7
1980	1.8	1.0	2.8	2.2	2.0	4.8
1981	2.4	1.3	0.8	1.4	1.2	2.4
1982	6.2	13.0	5.5	10.0	8.4	3.9
1983	1.0	0.9	1.2	2.0	1.4	3.7
1984	1.5	2.8	6.1	4.7	4.2	4.7
1985	2.1	3.7	0.8	5.6	2.9	2.8
1986	2.2	0.5	1.6	9.9	4.1	3.7
1987	2.5	12.1	0.8	6.4	4.8	3.9
1988	0.4	0.7	7.3	0.4	2.7	3.9
1989	2.9	97.8	19.4	2.2	25.2	10.9
1990	0.9	3.1	3.8	0.6	2.1	10.0
37-year mean	6.1	9.9	12.4	6.2	9.0	

Table 2. Habitat requirements for striped bass eggs, prolarvae, and juveniles. The critical period is April-June. Turbidity measured as total suspended solids except as noted.

Life Stage	Temperature °C	Salinity ppt	pH	Hardness mgL ⁻¹ CaCO ₃	Alkalinity mgL ⁻¹ CaCO ₃	Dissolved oxygen mgL ⁻¹	Turbidity mgL ⁻¹
EGG optimum	12-23 ^{48,55} 14-20 ¹⁶⁷ 18-21 ¹⁹⁷	0-8 ¹⁶⁶ > 0.5 ⁶⁶ 2-10 ^{20,116}	7.0-9.5 ^{20,116}	>150 ¹¹⁶	>150 ¹¹⁶	>5.0 ^{225,175,110}	<1000 ⁸
PROLARVA optimum	12-23 ⁵⁵ 18-21 ²⁰⁰	0-15 ¹ 1-3 ^{11,68} 3-7 ¹	7-8.5	>150 ^{20,116}	>150 ¹¹⁶	>5.0 (18°C)	<100 ⁸
POSTLARVA optimum	12-23 ⁵⁵ 15-22 ^{18,49}	0-15 ¹ 3-7 ¹ 1-14 ¹⁶⁷	7-8.5	>150 ^{20,116}	>150 ¹¹⁶	>5.0 (18°C)	<<500 ⁸
JUVENILE	10-27 ⁴⁹ 14-21 ^{124,49} 14-26 ⁴⁷	0-16 ⁵⁶ < 12 ¹²	7-9 ¹¹⁰	>150 ^{20,116}	>150 ¹¹⁶	>5.0 ¹²⁴	0-10 (clay/silt) 0-2000 (fine sed.)

Table 3. Summary of research conducted on factors responsible for the decline of striped bass in Chesapeake Bay. Modified from Rago *et al.*³¹

Hypothesis	Research	Summary
Contaminants	<i>In situ</i> and on-site bioassays in spawning rivers: Nanticoke, 1984-88; C&D Canal 1985-88; Choptank 1987-88; Potomac 1986, 1988.	Toxic conditions in some rivers in some years. No single contaminant is consistently responsible for mortality.
	Laboratory experiments; pH, aluminum and metals effects for various life stages.	Highly sensitive to pH 6.0 and dissolved aluminum. Salinity and organic acids ameliorate effects.
Starvation	Laboratory and field studies.	Limited evidence of impact except in Potomac and Choptank Rivers (first-feeding larvae only).
Fishing mortality	Extensive management changes; simulation modeling	Strong evidence of over-exploitation that reduced recruitment. Difficult to distinguish from effects of other factors.
Predation and competition (larval stage)	Exposed larvae to a variety of predators in laboratory studies	Numerous potential predators but evidence in field data is lacking.
Climatic events	Evaluated historical data on pH trends in major spawning rivers	No evidence of systematic decrease in pH or increased frequency in low pH events. Historical information is insufficient to detect small or episodic changes.
Water use practices	Evaluated flow conditions in vicinity of C&D Canal	Evidence of transport out of Bay and entrainment of larvae. Overall impact is uncertain.
Disease	Laboratory studies of IPNV	Non-lethal, but striped bass can act as carriers. Potential disease problems in intensive culture but much lesser problem in nature.

Table 4. Acute toxicity of selected elements, inorganic and organic compounds to striped bass. TRC = total residual chlorine; OPO = ozone-produced oxidants.

Substance	Life stage	Water type	Temperature °C	Effect	Concentration mgL ⁻¹	Reference
INORGANIC						
aluminum	larva	fresh		100% mort. (7 d)	0.30 (pH 5-7.2)	27
		fresh		97% mort. (7 d)	0.10 (pH 6.5)	27
		fresh		75% mort. (7 d)	0.10 (pH 7.2)	27
		fresh		100% mort. (7 d)	0.0 (pH 5.0-5.5)	27
		fresh		52% mort. (7 d)	0.0 (pH 6.5)	27
	juvenile	natural- soft, fresh	13.5-15.5	>90% mort.	~0.12 (pH 6.3)	79
		fresh		0% mort. (7 d)	0.30 (pH 6.5-7.2)	27
		fresh		100% mort. (7 d)	0.30 (pH 5.5)	27
		fresh		22% mort. (7 d)	0.0 (pH 5.5)	27
ammonium hydroxide	juvenile	saline	21	96 h LC ₅₀	1.9-2.85	88
arsenate	yolk-sac larva	saline	16-21.5	96 h LC ₅₀	18.69	119
	juvenile	saline	25-25.5	96 h LC ₅₀	18.96	119
arsenic	juvenile	fresh, soft	20±2	96 h LC ₅₀	40.50	179
		fresh, hard	20±2	96 h LC ₅₀	30.50	179
cadmium	larva	fresh	21	96 h LC ₅₀	0.001	105
	larva (1 d)	fresh	20	73-89% mort. (52 h)	0.20	243
	larva (7 d)	fresh	20	mort. (120 h)	0.005	243
	juvenile	fresh	21	96 h LC ₅₀	0.002	106
		fresh, soft	20±2	96 h LC ₅₀	0.004	179
		fresh, hard	20±2	96 h LC ₅₀	0.010	179
		1 ppt	20±2	96 h LC ₅₀	0.075	179
		fresh	20	290 h LC ₅₀	0.006	243
chloride	larva	fresh	21	96 h LC ₅₀	1000	105
	juvenile	fresh	21	96 h LC ₅₀	5000	106
chlorine (TRC)	egg	saline		48 h LC ₅₀	0.20-0.22	165
		saline	18-19.5	100% mort. (36 h)	0.06	72
		saline	17-19	0% hatch (40 h)	0.21	160
		saline	17-19	3.5% hatch	0.07	160
		saline	17-19	23% hatch	0.01	160
	larva	saline	18.5-19.0	96 h LC ₇₅	0.06	72
	egg	saline	18-19.5	11-22% mort. (36 h)	0.06-2.00	72
		saline	20-20.5	96 h LC ₃₉	2.0	72
chlorine	larva	saline	18.5-19.0	96 h LC ₅₀	0.14	75
		saline		96 h LC ₅₀	0.20	165
		saline	18	96 h LC ₅₀ (incipient)	0.07-0.40	160
		saline	18	96 h LC ₅₀	0.04	160
	juvenile	saline		96 h LC ₅₀	0.19	75
	juv. (60 d)	saline	24-25	96 h LC ₅₀	0.23	75
	juv. (388 d)	saline		96 h LC ₅₀	0.5	105
	larva	fresh	21	96 h LC ₅₀	0.25	105
chlorine (HTH)	juvenile	fresh	21	96 h LC ₅₀	28.0	179
chromium	juvenile	fresh, soft	20±2	96 h LC ₅₀	38.0	179
		fresh, hard	20±2	96 h LC ₅₀	58.0	179
		1 ppt	20±2	96 h LC ₅₀	100	105
potassium dichromate	larva	fresh	21	96 h LC ₅₀	75	105
	juvenile	fresh	21	96 h LC ₅₀	0.74	176
copper	egg	fresh	14-19	48 h LC ₅₀	0.05	105
	larva	fresh	21	48 h LC ₅₀	0.31	176
		fresh	14-19	96 h LC ₅₀	0.24	242
		saline	17	96 h LC ₅₀	0.05	106
		fresh	21	96 h LC ₅₀	4.3	195
	juvenile	fresh	17	96 h LC ₅₀		
		fresh	17	96 h LC ₅₀		
		fresh	17	96 h LC ₅₀		

STRIPED BASS

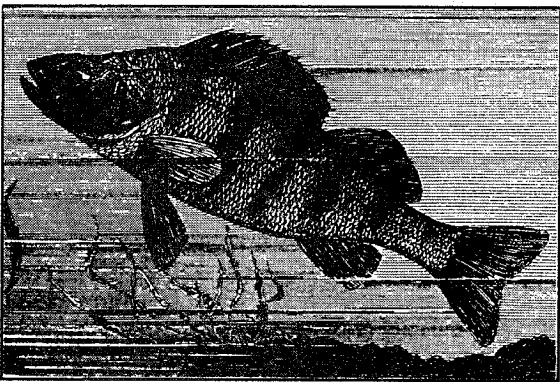
Substance	Life stage	Water type	Temperature °C	Effect	Concentration mgL ⁻¹	Reference	
copper sulfate	larva	fresh, soft	20±2	96 h LC ₅₀	0.100	179	
		fresh, hard	20±2	96 h LC ₅₀	0.270	179	
		1 ppt	20±2	96 h LC ₅₀	0.190	179	
		fresh	21	96 h LC ₅₀	0.1	105	
		fresh	21	96 h LC ₅₀	0.15	105	
		fresh	21-22	96 h LC ₅₀	0.6	114	
iron	larva	fresh	21	96 h LC ₅₀	0.62	234	
	juvenile	fresh	21	96 h LC ₅₀	4.0	106	
nickel	juvenile	fresh	21	96 h LC ₅₀	6.0	105	
	juvenile	fresh	17	96 h LC ₅₀	6.2	196	
ozone (OPO)	egg	fresh, soft	20±2	96 h LC ₅₀	3.9	179	
		fresh, hard	20±2	96 h LC ₅₀	33.0	179	
		1 ppt	20±2	96 h LC ₅₀	21.0	179	
		fresh	18.9-19.0	30 h LC ₅₀	0.06	73	
		3-5 ppt	17.4-17.5	30 h LC ₅₀	0.21	73	
		potassium permanganate	larva	fresh	21	96 h LC ₅₀	100
selenate	juvenile	fresh	21	96 h LC ₅₀	4.0	105	
		fresh	21	96 h LC ₅₀	2.6	114	
		fresh	21	96 h LC ₅₀	2.6	234	
		fresh	21	96 h LC ₅₀	9.79	119	
selenium	yolk-sac larva	saline	16-21.5	96 h LC ₅₀	13.02	119	
	postlarva	saline	16-21.5	96 h LC ₅₀	1.325	179	
sulfate	juvenile	fresh, soft	20±2	96 h LC ₅₀	2.4	179	
		fresh, hard	20±2	96 h LC ₅₀	1.550	179	
		saline	20±2	96 h LC ₅₀	250	106	
		fresh	21	96 h LC ₅₀	3500	106	
sulfur dioxide	egg	saline	18-19.5	8-21% mort. (36 h)	0.06-2.00	72	
	larva	saline	20-20.5	96 h LC ₅₀	2.0	72	
zinc	egg	fresh	14-19	48 h LC ₅₀	1.85	176	
	larva	fresh	21	96 h LC ₅₀	0.1	106	
		fresh	14-19	96 h LC ₅₀	1.18	176	
		saline	16	96 h LC ₅₀	9.2	16	
	juvenile	fresh	21	96 h LC ₅₀	0.1	106	
		fresh	17	96 h LC ₅₀	6.7	196	
		fresh, soft	20±2	96 h LC ₅₀	0.120	122	
		fresh, hard	20±2	96 h LC ₅₀	0.430	122	
		1 ppt	20±2	96 h LC ₅₀	0.430	122	
		ORGANIC					
	2-4,D butyl ester	larva	fresh	21	96 h LC ₅₀	0.15	105
		juvenile	fresh	21	96 h LC ₅₀	3.0	105
Abate	juvenile	saline	14	96 h LC ₅₀	1.0	122	
achromycin	juvenile	fresh	21-22	96 h LC ₅₀	190	114	
acriflavine	larva	fresh	21	96 h LC ₅₀	5.0	106	
	juvenile	fresh	21	96 h LC ₅₀	27.5	106	
		fresh	21	96 h LC ₅₀	16.0	235	
aldrin	larva	fresh	21	96 h LC ₅₀	0.01	106	
		saline	13	96 h LC ₅₀	0.0072	122	
		fresh	21	96 h LC ₅₀	0.075	106	
		fresh	20	96 h LC ₅₀	0.010	196	
amifur	larva	fresh	21	96 h LC ₅₀	10	106	
	juvenile	fresh	21	96 h LC ₅₀	30.0	106	
benzene	juvenile	saline	17.4	96 h LC ₅₀	10.9 µL L ⁻¹	159	
		saline	16	96 h LC ₅₀	5.8 µL L ⁻¹	16	
carbaryl	juvenile	saline	17	96 h LC ₅₀	1.0	122	
		fresh, soft	20±2	96 h LC ₅₀	0.760	179	
		saline	20±2	96 h LC ₅₀	2.3	179	
chlordan	juvenile	saline	15	96 h LC ₅₀	0.0118	122	
Co-Ral	juvenile	fresh	21	96 h LC ₅₀	62	235	
cutrine	juvenile	fresh	21	96 h LC ₅₀	0.1	106	

Substance	Life stage	Water type	Temperature °C	Effect	Concentration mgL ⁻¹	Reference
DDD	juvenile	saline	17	96 h LC ₅₀	0.0025	122
DDT	juvenile	saline	17	96 h LC ₅₀	0.00053	122
dibrom	juvenile	saline	13	96 h LC ₅₀	0.5	122
dieldrin	larva	fresh	21	96 h LC ₅₀	0.001	106
	juvenile	saline	14	96 h LC ₅₀	0.0197	122
		fresh	21	96 h LC ₅₀	0.25	106
diquat	larva	fresh	21	96 h LC ₅₀	1.0	106
	juvenile	fresh	21	96 h LC ₅₀	10.09	106
		fresh	21	96 h LC ₅₀	80	235
diuron (Karmex)	larva	fresh	21	96 h LC ₅₀	0.5	105,106
	juvenile	fresh	21	96 h LC ₅₀	6.0	105,106
		fresh	21	96 h LC ₅₀	3.1	234
Dursban	juvenile	saline	13	96 h LC ₅₀	0.00058	122
dylox	larva	fresh	21	96 h LC ₅₀	5.0	106
	juvenile	fresh	21	96 h LC ₅₀	2.0	105
		fresh	21	96 h LC ₅₀	5.2	234
endosulfan	juvenile	saline	16	96 h LC ₅₀	0.0001	122
endrin	juvenile	saline	17	96 h LC ₅₀	0.000094	122
EPN	juvenile	saline	18	96 h LC ₅₀	0.60	122
ethyl parathion	larva	fresh	21	96 h LC ₅₀	2.0	105
	juvenile	fresh	21	96 h LC ₅₀	1.0	105
		saline	15	96 h LC ₅₀	0.0178	122
fenthion	juvenile	saline	13	96 h LC ₅₀	0.453	122
formaldehyde	larva	fresh	21	96 h LC ₅₀	10	106
	juvenile	fresh	21	96 h LC ₅₀	15	106
		fresh	21-22	96 h LC ₅₀	20	114
		fresh	21	96 h LC ₅₀	18	234
heptachlor	juvenile	saline	13	96 h LC ₅₀	0.003	122
lindane	juvenile	fresh	21	96 h LC ₅₀	0.40	235
		saline	13	96 h LC ₅₀	0.0073	122
malathion	juvenile	fresh	21	96 h LC ₅₀	0.24	235
		saline	13	96 h LC ₅₀	0.014	122
		fresh	20	96 h LC ₅₀	0.039	196
		fresh, soft	20±2	96 h LC ₅₀	0.0245	179
		1 ppt	20±2	96 h LC ₅₀	0.065	179
methoxychlor	juvenile	saline	15	96 h LC ₅₀	0.0033	122
methyl parathion	larva	fresh	21	96 h LC ₅₀	5.0	105
	juvenile	fresh	21	96 h LC ₅₀	4.5	105
		saline	13	96 h LC ₅₀	0.79	122
		fresh	20	96 h LC ₅₀	14.0	196
oil field brine as chloride	juvenile	fresh	21	96 h LC ₅₀	75	104
roccal	larva	fresh	21	96 h LC ₅₀	0.5	106
	juvenile	fresh	21	96 h LC ₅₀	1.5	106
rotenone	larva	fresh	21	96 h LC ₅₀	0.001	106
	juvenile	fresh	21	96 h LC ₅₀	0.001	106
simazine	juvenile	fresh	21	96 h LC ₅₀	0.25	234
toluene	juvenile	saline	16	96 h LC ₅₀	7.3 µL L ⁻¹	16
tributyl tin (TBT)	larva (13 d)	saline	18-20	100% mort. (5 d)	0.002	185
	larva (16 d)	saline	18-20	100% mort. (6 d)	0.015	185
toxaphene	juvenile	saline	17	96 h LC ₅₀	0.0044	122
		fresh, soft	20±2	96 h LC ₅₀	0.005	179
		1 ppt	20±2	96 h LC ₅₀	0.0076	179
m-xylene	juvenile	saline	16	96 h LC ₅₀	9.2	16

YELLOW PERCH

Perca flavescens

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Yellow perch stocks in Chesapeake Bay have declined since the mid-1960's. The cause for the decline has not been identified precisely, but several environmental factors undoubtedly hinder stock recovery. They include sedimentation from improper land use, decreased spawning habitat caused by stream blockages, and the interaction of metals and acid rain. Eutrophication caused by excessive nutrient loading may adversely affect yellow perch by decreasing dissolved oxygen, which reduces the forage base for yellow perch.

Suitable habitat for yellow perch includes dissolved oxygen greater than 5.0 mgL⁻¹, summer water temperatures below 30°C, and gradually warming water temperatures during egg and larval development (March through May). Yellow perch populations appear able to sustain reproducing populations at pH 5.0, but pH 4.0 has been documented after rain events. Salinities above 2.0 ppt reduce hatchability of yellow perch eggs. Adults and juveniles tolerate salinities of 13.0 ppt.

Restoration of yellow perch to historic abundance levels may be accomplished by reducing sedimentation and eutrophication in the Bay. Toxic inputs also must be reduced, and suitable yellow perch spawning habitat must be restored by reducing stream blockage. Stock recovery also will require reduced mortality which can be accomplished primarily by proper management of the yellow perch fishery.

INTRODUCTION

Yellow perch is one of the most important fish species in the Chesapeake Bay. Yellow perch make their spawning run in late winter, thereby providing the earliest opportunity for sportfishermen to get into the field. The early spawning run has become an important tradition for many sportsmen. This late-winter spawn is equally important for commercial fishermen. Yellow perch are the first catchable commercial fish species of the year. The importance of yellow perch to commercial fishermen has been amplified in light of the moratoria on shad and striped bass harvest.

Chesapeake Bay once sustained a vigorous yellow perch fishery. Commercial fishermen harvested over one million pounds annually at the turn of the century.⁸ Since then

yellow perch landings have fluctuated, but by 1965, the commercial catch was only 278,000 pounds. Annual catches from 1967 to 1970 stabilized at about 110,000 pounds. Yellow perch catches declined precipitously from 1973 through 1986. Recently, annual catches have exceeded 40,000 pounds (Table 1). This increase in landings is attributed to increased fishing effort, not to a population increase. Since the early 1980's, most of the commercial fishing effort has been centered in the upper Chesapeake Bay.

Yellow perch have become a more important catch for commercial fishermen since moratoria have been imposed on striped bass and shad fishing in Maryland. Prices for yellow perch, adjusted for inflation, were stable at \$0.11 per pound in the mid-1970's, but increased to \$0.15 per pound in the mid-1980's.⁶⁶ Unadjusted prices for

YELLOW PERCH

yellow perch were approximately \$1.00 per live pound in 1988, 1989, and 1990.

Total 1990 February income for Maryland yellow perch commercial fishermen was \$20,000 (unpublished data: Maryland Department of Natural Resources). The February catch represents less than one-half of the total annual commercial catch of yellow perch, which is estimated at \$60,000.

The value of the recreational fishery is extremely hard to determine. The economic value has been reported as the marginal willingness to pay: the amount of money that a fisherman would pay to catch one yellow perch. In 1983, the marginal willingness to pay for yellow perch was \$0.50 in Maryland.⁶⁶ The authors multiplied this figure by the estimated sportfishing harvest during the non-spawning season, and estimated the yearly value of the Maryland yellow perch sportfishing industry at \$120,000.

BACKGROUND

The yellow perch is a member of the family Percidae. The family contains 121 species, of which approximately 100 are found in North America. Percids are found throughout the northern hemisphere excluding Alaska, the western United States, extreme northeast Canada, Greenland, and Iceland.¹ In the U.S., the percids are represented by the yellow perch, sauger, walleye, and darters.

Yellow perch range from South Carolina north to Nova Scotia, west through the southern Hudson Bay region and Saskatchewan, and south to the northern half of the Mississippi drainage.⁶⁶ In Maryland, yellow perch historically have been reported in all tributaries to Chesapeake Bay (Map Appendix) and the Youghiogheny River system (Ohio River drainage). There has been an absence of spawning in several lower western shore Chesapeake Bay tributaries over the past several years.⁵⁷

Available data suggest that yellow perch populations are declining, although the rate of decline varies in different parts of the Chesapeake Bay. Spawning occurs in upstream reaches of most rivers that hold adult yellow perch (Map Appendix). Small spawning runs of yellow perch were found in these western shore rivers: North River, Magothy Run, and Severn Run.³⁷ No spawning yellow perch were captured in Stockett's Run (Patuxent River drainage) nor in Bacon Ridge Branch (South River drainage), and only nine adult yellow perch were collected during the spawning run in the North River.²³ The coordinated juvenile survey collected only five juvenile yellow perch in Mattawoman Creek, and none in the South or Severn Rivers.

A similar study found few spawning yellow perch on two Chester River tributaries: Granny Finley Branch and Three

Bridges Branch.³¹ Juvenile yellow perch have been collected in the Potomac River system from Washington, D.C. downstream to Breton Bay in St. Mary's County, Maryland. Absences of yellow perch were noted in the Rhode River and the lower West River.⁵⁷ Conversely, yellow perch are more prevalent in the upper Bay. All upper Bay tributaries have been found to hold juvenile yellow perch; the Bush, Sassafras, Northeast, Back, and Middle Rivers produce the majority of the landings for the fishery in the upper Bay.⁵⁷

LIFE HISTORY

Migration and spawning

Adult yellow perch migrate from downstream stretches of tidal waters to spawning areas in less saline upper reaches in mid-February through March. Males tend to reach the spawning areas first.^{66,77} Spawning takes place generally in mid-March, but the actual spawning date is influenced greatly by water temperatures. Optimal spawning temperatures were reported as 7.8-12.2°C.³² Yellow perch spawning was documented at 2.0°C in the Severn River, but peak yellow perch spawning occurred in the Patuxent River at surface temperatures of 8.0-10.0°C.⁷⁷ Eggs are partially extruded and dragged through expelled milt. Fertilization may be accomplished by multiple males. As many as 25 males have been observed to fertilize a single egg strand.⁷⁷

Eggs

Eggs and larvae are sensitive to several environmental factors including temperature,²⁸ pH and aluminum interactions,⁷⁵ sedimentation,² and loss of habitat. Therefore, the Chesapeake Bay Living Resources Task Force identified eggs and larvae as the critical life stages for yellow perch in Chesapeake Bay.¹⁰

Individual eggs are semi-demersal and clear amber. The average diameter of eggs before water hardening is 1.76 mm; post-fertilized eggs have a mean diameter of 2.26 mm.⁴⁶ The single oil droplet averages 0.4 mm.¹

Eggs are laid in a conspicuous gelatinous strand from 0.6 to 2.0 m long.¹ Egg deposition occurs in upstream areas generally in places with large amounts of organic debris.⁶⁶ Riparian litter may serve as attachment sites for the adhesive egg strands. Despite the distinctiveness of the egg strand, there appears to be no predation on developing eggs. Either egg masses are unpalatable or predators do not recognize the egg strands as a food source.⁵⁶

Development

Egg development stages were broadly defined by Mansueti.⁴⁶ Yolk completely filled the perivitelline space prior to fertilization. The oil droplet was displaced to the periphery, and germinal tissue formed around the droplet 14 minutes after fertilization. The two-cell stage was evident five hours after fertilization. Gastrulation occurred 21

hours after fertilization; at this stage, germinal ring covered one-third of the yolk. The author identified "early embryonic stages" at three to six days after fertilization. These stages were terminated by the separation of the tail from the yolk. Pectoral buds, auditory vesicles, and caudal finfolds were present after 6-11 days. Myotomes were fully present and the vent was visible by day 16. Eyes formed and the heart was functional during the period from 16-25 days. Hatching occurred 25-27 days after fertilization.

Larvae

Yellow perch are considered prolarvae from hatching until the yolk sac is completely resorbed. Yellow perch hatch at 5-8 mm.¹ There are 32-42 myomeres (body segments). The prolarvae remain near cover. Swim bladder inflation, which is crucial for normal development, occurred at 7 mm.⁴⁶ Swim bladder inflation also was reported at the swim-up stage at 13.0°C.³³ Yolk sac is completely resorbed at 8-10 mm and bones begin to ossify. At 11-15 mm, fin rays are evident. Larval yellow perch in Lake Itasca migrated offshore for their larval existence to reduce risks from littoral predators.⁸¹ My observations in the Wye River and at hatchery ponds seem to verify offshore existence for larval yellow perch in Chesapeake Bay as well.

Juveniles

Fish are considered juveniles when all finfolds are developed. Essentially, juveniles are identical to adults except in size. Yellow perch are considered juvenile at about 20-40 mm total length (TL). Scales appear at 20-22 mm TL. In general, juvenile yellow perch migrate from the limnetic zone to the littoral zone.⁸¹ This behavior evolved to enable juvenile yellow perch to feed on the comparably richer near-shore food sources. At this stage, predator avoidance should be sufficiently developed to reduce predation risks.

Adults

Analysis of age distributions of yellow perch shows that the age structure of the spawning population has changed over the past three decades. Yellow perch collected from the Severn River in the early 1960's showed that ages II through X were equally represented.⁵³ Recent studies demonstrate that only a few year classes are represented in the commercial catch (Table 2).^{17,18} The major implication of the absence of older fish is decreased reproductive output per spawning fish.

The age when fish first mature depends proximally on growth rate and ultimately on variables such as forage base and competition. Females matured by age III in the Severn River, and some males matured at age I. All male perch were mature by age III.⁵³

Fecundity, or the amount of eggs that a female produces, varies with body length and weight. This is a fundamental

parameter that is important in projecting production estimates. Unfortunately, the only estimates of fecundity relationships for Chesapeake Bay stocks of yellow perch are 20-30 years old, and changes in forage base and growth rate may have made these equations obsolete.

The fecundity of Patuxent River yellow perch was best described by the equation:

$$\text{fecundity} = 150.56(\text{weight in g}) - 1424.1.$$

Fecundities of yellow perch were 5,266-75,715 eggs per female in the Patuxent River⁷⁴ and 5,900-109,000 eggs per female in the Severn River.⁵³

Sex ratios of yellow perch may deviate drastically from the expected 1:1 (M:F) ratio. Sex ratios have been reported from several Chesapeake Bay tributaries (Table 3). Deviations from a 1:1 sex ratio may be caused by the different migration patterns of the sexes. Male yellow perch reach the spawning areas before females and do not migrate downstream until the females leave the spawning areas.⁷⁷

Growth characteristics

Comparisons of growth rates of yellow perch in Chesapeake Bay (Tables 4 and 5) and in impoundments, the Great Lakes, and other freshwater systems^{19,21,55,78} indicate that in both freshwater and Bay populations, females were consistently larger than males at any given age, and that Chesapeake Bay growth rates were similar to those reported from the Great Lakes.⁶⁶

Several studies have found a variety of factors that affect growth rates. Some studies showed that yellow perch growth rates were density dependent in the upper Great Lakes,^{29,39,78} but not in western Lake Erie.²⁶ Other studies showed that inter-basin differences in Lake Erie's forage base accounted for differential growth rates,²⁷ that different diets may alter growth by as much as 300%,¹³ and that lake morphology, or the shape and contour of a lake, played the most important role in determining growth rates in Lake Itasca, where growth rates varied directly with the amount of littoral zone.⁸¹ Physiologically, temperature is one of the most important physical variables for fish, but there did not appear to be a correlation between rising temperatures and yellow perch growth in South Bay, Lake Huron.²⁹

Migrations

Adult yellow perch remain in their natal river systems. In a two-year study, yellow perch from the Severn and Chester Rivers were captured, tagged, and released in the Severn River. Tag returns showed that all of the native Severn River yellow perch were recaptured within the Severn River system, whereas the stocked yellow perch from the Chester River were recaptured throughout Chesapeake Bay.⁴⁷

The only migration evident besides adult spawning migration is the downstream dispersal of juvenile yellow perch. Neither the timing nor the extent of this migration has been studied, but one study indicated that juveniles do not disperse downstream synchronously.¹⁸ Some juvenile yellow perch were collected in early June in the brackish waters of the Wye East River in Maryland where maximum water depths were four feet (1.2 m) and salinity was 12.2 ppt, whereas other juveniles were collected further upstream in late September.

ECOLOGICAL ROLE

Although the feeding habits of yellow perch have been studied extensively in freshwater systems, little information has been found on the diets of estuarine yellow perch. Freshwater stocks of yellow perch change prey selection as they develop. In a Lake Itasca study, post-yolk sac larvae fed on limnetic zooplankton.⁸¹ First foods for these fish (9 mm TL) were copepods and cladocerans. Ghost midges were eaten as the larvae grew. Newly metamorphosed juveniles continued to feed on pelagic plankton but quickly shifted to benthic invertebrates. Cannibalism may account for 25% of the juvenile yellow perch diet.⁵⁹ Cannibalism of juvenile yellow perch in hatchery ponds also has been documented.¹⁸

Adult yellow perch in Chesapeake Bay fed primarily on anchovies, killifish, and silversides.³⁰ Susquehanna River yellow perch consumed scuds, caddisfly larvae, and midge larvae.⁷⁹ A study in the Gunpowder River determined that midge larvae were the preferred food for adult yellow perch.⁶⁶ Differences among these studies probably were due to different forage bases rather than different behavioral responses of yellow perch.

Yellow perch are eaten by top predators. Predators on yellow perch in Chesapeake Bay have not been thoroughly documented,⁶⁶ but during Maryland Department of Natural Resources (DNR) yellow perch collections, striped bass, largemouth bass, chain pickerel, catfish species, white perch, and bluefish were found in the same areas as yellow perch. Yellow perch larvae are important prey for alewives in Lake Ontario,⁵ which also could be true in the Chesapeake Bay region, because yellow perch hatching dates in the Bay coincide with alewife and blueback herring upstream spawning migrations. Piscivorous birds, including ospreys, bald eagles, several species of gulls, terns, herons, and egrets have been noted at many yellow perch sampling stations.

HABITAT REQUIREMENTS

Water Quality

Water quality factors that affect Chesapeake Bay stocks of yellow perch are discussed in the following sections.

Table 6 lists the most important characteristics and tolerance limits for each life history stage.

Temperature

Temperature is the most important environmental factor for poikilothermic (cold-blooded) animals. It controls metabolic rate, growth, and reproduction. Many studies show how temperature directly affects yellow perch and how temperature changes may cause behavioral changes which ultimately could induce mortality.

Gradual warming ($0.9^{\circ}\text{C d}^{-1}$) is important to maintain constant and normal development of eggs.²⁸ Hatching times are greatly influenced by temperature: eggs reared at 5.4°C incubated in 51 days with 50% mortality,³⁴ compared to 27 days at 8.3°C ²⁵ and 8-11 days at 18°C .⁶⁹ The last value is most typical of water temperatures at hatching dates in the Chesapeake Bay region.

After hatching, larvae have a temperature tolerance range of $10\text{--}30^{\circ}\text{C}$.^{28,33} Significant larval mortality occurred when temperatures were increased 15°C for larvae acclimated at $13.5\text{--}17^{\circ}\text{C}$. Four-hour exposure of larvae to temperatures from $19\text{--}24.5^{\circ}\text{C}$ produced no significant effects.⁶¹ The acclimation temperatures are applicable to Bay area larvae, which were most frequently captured in water of $8\text{--}17^{\circ}\text{C}$.¹⁵

The temperature tolerance of juveniles is similar to that of larvae. Several studies have found that juveniles selected a temperature range of $19\text{--}24^{\circ}\text{C}$.^{9,34,50,54,80} Two studies determined that juveniles demonstrate a diel or semi-daily temperature preference: 16.7°C just before dawn and 23.8°C at dusk.^{4,65} Young of the year yellow perch grew optimally at constant temperatures between $26\text{--}30^{\circ}\text{C}$, did not grow at 8°C , and died at 34°C .⁵¹

Adults have thermal preferences similar to juveniles,^{3,52} with 24.7°C apparently the physiologically optimal temperature.³⁴ Two studies conducted in Lake Erie found that adults tolerated a temperature range of $12\text{--}16^{\circ}\text{C}$ during the winter and $16\text{--}22^{\circ}\text{C}$ from June through September.^{20,64}

Sublethal and behavioral responses of juvenile fish to temperature are probably very important in determining suitable habitat, but few studies have addressed sublethal effects or attempted to correlate the implications of sub-optimal temperature with actual field observations. Thermal avoidance may cause larval and juvenile perch to emigrate from areas that provide cover from predators, or it may exclude young perch from foraging in areas with high prey densities. Also, should ambient temperatures decrease growth rates, the chances of being preyed upon would be considerably greater.

Dissolved Oxygen

Molecular oxygen is required for respiration by all higher animals. Fish extract oxygen that is dissolved in water. Dissolved oxygen (DO) passes across the gills and is extracted from the water by simple diffusion. The minimum suitable DO concentration for all life stages of yellow perch is 5 mgL^{-1} .³⁸ However, each life history stage has different oxygen requirements, and seasonal oxygen requirements may not always be equivalent.

Seasonal lethal DO for adults is 0.2 mgL^{-1} in winter and 1.5 mgL^{-1} in summer.⁷⁶ Yellow perch require less oxygen in winter because they are poikilothermic, that is, their metabolism is determined by ambient temperature. Yellow perch are much less active in low winter temperatures and consequently they need less oxygen.

The lethal DO for larvae at 23°C was 0.84 mgL^{-1} , but water temperatures are generally lower than 23°C during larval stages. A dissolved oxygen concentration of 0.84 mgL^{-1} was not lethal for young of the year at 15.1°C .⁵⁹ Dissolved oxygen less than 7 mgL^{-1} was lethal to juveniles in Lake Erie.⁷⁶ Growth of juveniles is not significantly affected when mean DO concentrations are more than 3.5 mgL^{-1} , but is reduced significantly when DO concentrations are less than or equal to 2.0 mgL^{-1} .⁷

Suboptimal DO may have many acute implications. If DO in a preferred habitat is below optimum, fish may leave the area, which could subject them to predation. Similarly, if growth is retarded, especially in the juvenile stage, survivability is reduced. For these reasons DO is one of the most important environmental requirements. A DO of 5 mgL^{-1} is viewed as the lowest average concentration that sustains normal development and activity.

Salinity

Many Chesapeake Bay stocks of yellow perch are subjected to some degree of salinity in one or more life history stages. Yellow perch spawn in areas with 0-2.5 ppt salinity.⁵³ The optimal salinity range for yellow perch reproduction is 0-2.0 ppt.^{25,38} An inverse relationship exists between hatching and salinities above 3.0 ppt. Larval mortality was lower in 3.0 ppt water than in 6.0 ppt water; however, mortality was 100% in 12 and 24 ppt water.⁶⁹ This relationship suggests that there is an optimum salinity for developing yellow perch, but growth efficiencies in different salinities have not been determined.

Juveniles exhibit a salinity tolerance range of 0-13 ppt.³⁸ Juveniles collected in the Miles and Severn Rivers were most abundant in 5-7 ppt.^{17,53} Those collected in the Wye River system were most often found in salinities of 6-8 ppt.¹⁸ Adult salinity tolerance is similar to that of juveniles, although preferences have not been determined in the

laboratory. Most field and literature review surveys list salinity tolerances from 0-13 ppt^{38,6} or from 0-10.3.^{16,53}

pH

Acidity, represented by low pH, has severe effects on aquatic ecosystems. Acidic conditions may cause reproductive failure in fish populations, or if severe enough, the death of individuals. Acidic conditions sometimes occur naturally, and sometimes are associated with mine drainage. In the Chesapeake Bay region, acid rain is the largest source of acidic input.

Many of the Bay's tributaries are poorly buffered,¹⁴ which exposes them to acidic runoff associated with atmospheric deposition. In a recent study of the combined effects of acidity and dissolved aluminum in flow-through bioassays with four pH levels and five aluminum concentrations, mortality rates were significantly greater in the lowest pH treatment (pH 5.0). Changes in aluminum concentration did not increase mortality.³⁷

Newly hatched yellow perch appear to be slightly more sensitive to acidity than older fish. Klauda *et al.*⁴² found that larvae could survive exposure to pH 5.0 for 24 h, but pre-feeding larvae were less sensitive than older larvae. Another study found that newly hatched yellow perch exhibited statistically significant differences in mortality when subjected to pH levels of 5.0.¹⁴ Addition of $100 \mu\text{gL}^{-1}$ aluminum at pH 5.0 also significantly increased larval yellow perch mortality.⁷⁵

Based on these studies, critical acidic conditions for egg and larval yellow perch occur at pH 4.5-5.5 with monomeric aluminum concentrations of $50\text{-}150 \mu\text{gL}^{-1}$.⁴¹ Yellow perch are assumed to be able to support reproducing populations when mean pH is 5.0.

Suspended sediments

Sediment loading may affect yellow perch reproduction. If sediment adheres to eggs, oxygen transport across the membrane may be reduced. Waterfront development and other human activities such as road construction cause increased sediment loads in spawning streams. Fine-grained suspended sediment in concentrations $\leq 500 \text{ mgL}^{-1}$ had no effect on yellow perch hatching success, but hatching time was delayed 6-12 h.⁷¹ Other tests determined that a 1000 mgL^{-1} suspension significantly reduced hatching success of yellow perch eggs,⁷⁰ although a similar study found no decrease in hatching success.²

Minimal information exists concerning the effects of suspended solids on larvae. The mechanisms of reducing larval survival are the same as with eggs. Fine-grained sediment may critically damage sensitive structures such as the gills and gill membranes. Survival was reduced significantly when larvae were exposed for 96 h to concentrations of suspended solids $\geq 500 \text{ mgL}^{-1}$.²

Structural habitat

Habitat Structure

Larvae inhabit the littoral zone immediately after hatching, but soon migrate to the limnetic zone and become pelagic.⁸¹ They are photopositive and migrate vertically through the water column.⁷⁶ Juveniles (25 mm) migrate back to the littoral zone⁸¹ and exhibit photonegative behavior.⁷⁶ Areas with > 20% cover were preferred by juvenile yellow perch.⁶⁶ Adults inhabit slow-moving, near-shore water with moderate cover.

Stream Velocity

Yellow perch fry generally inhabit currents less than 2.5 cm s⁻¹.⁶⁶ Adults prefer stream velocities > 5 cm s⁻¹. Currents in excess of 25 cm s⁻¹ shear egg strands.

SPECIAL PROBLEMS

Eutrophication

Eutrophication - the effect of excess nutrients on an aquatic system - affects fish populations by altering the physical properties of the water (e.g., increased water temperature and decreased DO) and by altering predator and prey community structures. Hypereutrophy in Lake Erie's western basin caused decreased yellow perch growth rates.²⁷ Yellow perch populations in the mildly eutrophic central basin showed increased growth rates. The authors attributed these differences to a shift in available benthic prey size. Hypereutrophy decreased benthic prey size in the western basin, whereas mild eutrophication in the central basin increased prey size. This shift was hypothesized to affect growth rates of larger yellow perch, eventually causing stunting.

Another study reported similar effects. In general, as eutrophication increased, prey sizes decreased, parasitism increased, and percid growth increased to a threshold level where further eutrophication decreased growth rates. Low dissolved oxygen concentrations due to eutrophication also caused shifts in percid distributions.⁴³

Acid Rain

Yellow perch are designated as acid tolerant; however, dissolved aluminum and depressed pH adversely affect larval yellow perch survival.⁷⁵ Spring pH levels below 5.0 have been documented in yellow perch spawning streams following rain events.⁵⁷ Acid deposition may not be the ultimate cause of declines of anadromous fish stocks, but it may inhibit recovery of fish populations.²³ Several ongoing studies are attempting to monitor the impact of acid deposition on spawning anadromous fish species. Passive and mechanical liming of spawning streams is being evaluated as a possible solution to the acidification problem.

Overharvest

Yellow perch congregate in upstream stretches of spawning streams during a contracted time period, a period when they feed aggressively. This spatial and temporal distribution of spawning behavior makes yellow perch more vulnerable to overharvesting by sportfishermen.

Commercial fishing for yellow perch is similarly affected by the contracted spawning runs. Fyke nets, the most common gear used in the commercial fishery, are very efficient in capturing migrating yellow perch. The ban on shad and striped bass fishing in Maryland has made yellow perch fishing more popular, which has led to increased landings in the upper Bay area.

Yellow perch populations should be able to sustain a healthy fishery but natural reproduction must be monitored carefully.

Contaminants

Acute toxicity tests of a number of inorganic and organic compounds have been conducted on yellow perch larvae and juveniles. Apparently no information is available on the toxicity of metals and metalloid elements to yellow perch, except for the studies of aluminum toxicity summarized above under **pH**.

Chlorine (total residual) is lethal to yellow perch larvae at moderately low concentrations (0.55 mgL⁻¹ and greater). Its toxicity increases with temperature, with exposure time, and with salinity.^{61,72} Effects of total residual chlorine on juveniles were similar; 24 h LC₅₀ ranged from 8 mgL⁻¹ at 10°C to 0.7 mgL⁻¹ at 30°C.⁶

Hydrogen sulfide is toxic to larvae and juveniles at very low concentrations, with 96 h LC₅₀ ranging from < 2 µgL⁻¹ for larvae at 20°C to 36 µgL⁻¹ for juveniles at 10°C.²²

The 96 h LC₅₀ for juvenile yellow perch exposed to hydrogen cyanide was 90.4 µgL⁻¹ at 15°C and 108 µgL⁻¹ at 21°C. Sensitivity to HCN increased with decreasing DO concentration.⁷⁴

Organic compounds for which toxicity information is available include a selection of pesticides and industrial chemicals (Table 7). It is difficult to generalize the relative toxicities of these compounds, except to comment that some insecticides (e.g., DDT, endrin, toxaphene, azinphos-methyl) are lethal at extremely low concentrations. Among Chesapeake Bay species, yellow perch may be particularly susceptible to chemical spills and contaminated runoff during the spawning and larval development periods, because of their concentration in relatively small streams.

Yellow perch exposed to ambient levels of a polychlorinated biphenyl (PCB; Arochlor 1016) in the Hudson

River accumulated tissue concentrations 10,400 times those in the river water.⁷³ Accumulation of PCB and other persistent organic compounds either directly or through the food chain could be a matter of concern for Chesapeake Bay yellow perch.

Stream Blockages

One cause of decreased suitable yellow perch spawning habitat is stream blockages. Many of the Bay's tributaries are impounded by gauging stations, highway culverts, small-scale dams, and hydroelectric facilities. A regional Chesapeake Bay effort is underway to mitigate the blockages by removing them or by installing fish passageways and diversions. The increase in available spawning and nursery habitat should serve to further rehabilitation of the stock.

Stream blockages are being breached in the Patapsco River drainage (6 blockages), the Susquehanna River (Conowingo Dam), the Elk River (one dam), the Bush river (two dams), and the Potomac River drainage (five dams). Other catalogued impoundments are in the Sassafras River drainage, Tuckahoe Creek, and the Chester River system.¹¹ Similarly, Virginia has developed a database of stream blockages. Embury dam on the Rappahannock River, five dams on the James River, and four dams on the Appamatox River are considered priority blockages (Map Appendix).¹¹

RECOMMENDATIONS

Nutrient inputs and other allochthonous and xenobiotic inputs that cause decreased DO levels in the Bay should be reduced.

Implementation and enforcement of programs to reduce both sediment and nutrient inputs into the Chesapeake system should be carried out to enable yellow perch stocks to expand in both range and abundance. Shoreline development and activities causing erosion and non-point source nutrient loading should be limited throughout the Chesapeake Bay drainage.

Harvest by sportfishermen and commercial fishermen must be monitored and managed, ideally by river system. Spawning stock characteristics such as age and growth rates must be determined to ensure that harvest levels are allowing sufficient reproduction to increase stock abundance. Size limits should be set to allow increased natural reproduction in the river systems open to yellow perch

fishing through greater spawning contribution of older age class fish.

Stream blockages that impede upstream spawning migrations must be removed or made passable to yellow perch.

Relatively little is known about yellow perch environmental preferences and tolerances in the Chesapeake Bay. This report draws largely from research literature on freshwater stocks of yellow perch. There is an urgent need for more research on estuarine stocks of yellow perch. This is especially true for larval and juvenile yellow perch habits and habitats.

The potential threat to yellow perch spawning runs and early life stages from improper use, disposal, and storage of pesticides and other toxic chemicals should be recognized.

Aggressive research must be continued on acid deposition. Mitigation efforts are also important through reduced sulfur emissions from industry and automotive exhaust. Evaluation of stream liming programs to make more areas suitable for spawning should be studied.

CONCLUSIONS

The ultimate, historical cause of the yellow perch population decline in the Chesapeake Bay has not been identified. Many environmental factors are acting to preclude yellow perch stock recovery. Loss of spawning habitat caused by stream blockages and sedimentation also undoubtedly are acting against yellow perch stock recovery, as are the synergistic effects of acid deposition and dissolved metals.

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YELLOW PERCH

Table 1. Commercial landings for yellow perch in Maryland, 1964-1986⁹

Year	Landings (lbs.)
1964	160,694
1965	278,548
1966	217,494
1967	184,103
1968	134,732
1969	123,397
1970	110,560
1971	92,362
1972	107,500
1973	37,000
1974	41,900
1975	38,200
1976	23,900
1977	18,100
1978	29,000
1979	25,200
1980	28,000
1981	15,145
1982	29,371
1983	40,943
1984	48,276
1985	43,849
1986	41,413
1987	50,264
1988	87,418
1989	65,260
1990	66,610

Table 2. Age composition of yellow perch collected from several Chesapeake Bay tributaries.

AGE CLASS								
River	Year	II	III	IV	V	VI	VII	VIII
Bush	1988 ¹⁸		11	17	15			
	1987 ³¹	23	43	16	14	1		
Sassafras	1988 ¹⁸		9	26	9	4	1	
	1987 ³¹		33	26	21	6		
Choptank	1988 ¹⁸	9	268	9	2	21	19	
	1987 ⁸	31	10	3	23	40	1	
	1986 ⁷		9	23	34	16	18	9

Table 3. Sex ratios of yellow perch collected from various Chesapeake Bay tributaries.

River	Year	Sex Ratio (M:F)	N
Bush	1988 ¹⁸	2.6:1	228
	1987 ³¹	0.92:1	96
Sassafras	1988 ¹⁸	1.1:1	99
	1987 ³¹	0.67:1	85
Choptank	1988 ¹⁸	1.5:1	334
	1987 ⁸	1.2:1	201
	1986 ⁸	0.68:1	153
Patuxent	1970 ⁷⁷	1.1:1	600

Table 4. Mean length at age (mm) for yellow perch collected from Chesapeake Bay tributaries.

River	Year	AGE CLASS					
		II	III	IV	V	VI	VII
Bush	1988 ¹⁸		197	212	211		
	1987 ³¹	186	219	236	245	250	
Sassafras	1988 ¹⁸		199	224	226	230	
	1987 ³¹		218	227	231	233	
Choptank	1988 ¹⁸	176	192	213	218	227	238
	1987 ⁸	159	189	208	218	244	
	1986 ⁸		190	212	230	242	238

Table 5. Length/weight and length/age regression equations of yellow perch from selected Chesapeake Bay tributaries. Length in mm, age in years, weight in g.

Length versus Age ³¹	
Bush River	
Sexes combined	length=237[1-e ^{-0.725(age)}]
Sassafras River	
Sexes combined	length=234[1-e ^{-0.886(age)}]
Length versus Weight ⁸	
Choptank River	
Males	log weight = 319(log length)-10.52
Females	log weight = 319(log length)-12.32

YELLOW PERCH

Table 6. Suitable water quality parameters for various life stages of yellow perch (NA = not available).

Life Stage	Temperature ^a °C	Salinity ppt	pH	Dissolved Oxygen mgL ⁻¹	Suspended Solids mgL ⁻¹
Egg	7-20	0-2	6-8.5	NA	<1000
Larvae	10-30	0-2	6-8.5	NA	<500
Juvenile	10-30 ^b	0-5	6-8.5	>5.0	NA
Adult	6-30	0-13	6-8.5	>5.0	NA

^a Optimum temperature ranges are dependent upon acclimation conditions.

^b Growth has occurred at temperatures below 10°C.³³

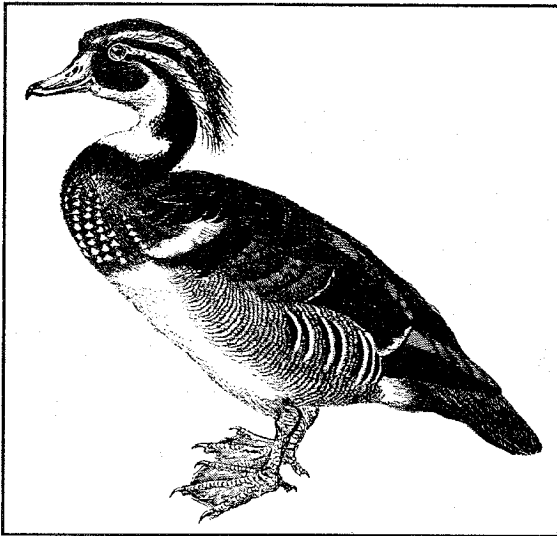
Table 7. Summary of acute toxicity of organic compounds to yellow perch larvae and juveniles. All values are 96 h LC₅₀. Ranges resulted from tests conducted under a variety of experimental conditions (temperature, pH, hardness, and formulation of the toxicant). All values except those indicated are from Mayer and Ellersieck.⁴⁹ Life Stage: L = larvae; J = juvenile.

Compound	Use	Life Stage	Range of Toxicity µg/L ⁻¹	Reference
acephate	insecticide	L	>50000->100000	
aminocarb	herbicide	L	230-11700	
antimycin A	piscicide	L	0.40	
azinphos-methyl	insecticide	L	2.4-40	
captan	fungicide	L	120	
carbaryl	insecticide	L	120-13900	
		J	1420	
chlordane	insecticide	L	9.6	
DDT	insecticide	L	9.0	
d-trans allethrin	insecticide	L	9.9	48
		J	9.9	
diflubenzuron	insecticide	L	>25000->50000	
dimethrin	insecticide	L	28	48,49
dinatrium	herbicide	L	780-1000	49,58
diquat	herbicide	L	23500-60000	
endrin	insecticide	J	0.15	
fenitrothion	insecticide	L	2000-5800	
fenthion	insecticide	L	1650	
folpet	fungicide	L	177	
Houghto-Safe 1120	hydraulic fluid	L	500	
leptophos	insecticide	L	7.0-3750	
malathion	insecticide	L	263	
methoxychlor	insecticide	L	17.5-50	
methyl parathion	insecticide	L	3060	
mexacarbate	insecticide	L	8300-16900	
mirex	insecticide	L	>100000	
paroil 1032	plasticizer	L	>5000	
paroil 1048	plasticizer	L	>10000	
paroil 160	coolant	L	>10700	
Arochlor 1016	industrial (PCB)	L	240	
Arochlor 1242	industrial (PCB)	L	>150	
Arochlor 1248	industrial (PCB)	L	>100	
Arochlor 1254	industrial (PCB)	L	>150	
Arochlor 1260	industrial (PCB)	L	>200	
phoxim	insecticide	J	563-710	
phthalate dibutyl	plasticizer	L	350	
Pydraul 50E	hydraulic fluid	L	540	
pyrethrum extract	insecticide	L	44.5	48
		J	33	
resmethrin		J	0.51	
RU-11679	insecticide	L	0.06	48
		J	0.06	
S-bioallethrin	insecticide	L	7.8	48,49
SBP-1382		L	0.5	48
toxaphene	insecticide	L	12	
trichlorfon	insecticide	L	>10000	
tricresyl phosphate	industrial	L	500	
xylene dimethylamino	metabolite	L	100-3400	

WOOD DUCK

Aix sponsa

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Threatened with extinction by habitat loss and unregulated hunting near the turn of the century, the wood duck has recovered to become one of our most abundant game ducks. A widely distributed species of forested wetland habitats, the wood duck is an abundant fall and spring migrant - the most abundant breeding anatid in the Chesapeake Bay drainage. The species' primary habitats are interior bottomland hardwood forests and adjoining river and bay marshes. Wood ducks also occupy habitats extending from tidal-brackish bay marshes to the very tops of watersheds, including the smallest of watercourses and temporary and seasonal pools within flood plain forests. Wood ducks are well-known for their beautiful plumage, dependence on tree cavities for nesting, and colonial roosting habit, especially in fall.

Although protection of large contiguous bottomland hardwoods and large riverine marshes is crucial to main-

tenance of wood duck populations within the Bay region, conservation of wetlands and riparian forest (along even the smallest of watercourses) will protect the diversity of habitats beneficial to wood ducks. Emphasis should be placed on managing riparian timber for mature and old growth, and especially to produce mast-bearing and cavity-producing species. Channelization and other actions that alter natural hydrology or habitats along watercourses are detrimental to wood ducks. Prudent management also includes conservative harvest limitations for maintenance of an abundance of wood ducks in the future.

INTRODUCTION

The wood duck is considered by many to be the most beautiful waterfowl in North America. Indeed, a literal translation of its scientific name, *Aix sponsa*, means a waterbird in bridal dress.¹⁷ It is apparent from many early accounts that the great beauty, wide distribution and abundance (especially in summer when other waterfowl are absent), and excellent eating quality of this bird captured the attention of ornithologists, naturalists, and wildfowlers during the colonial and post-colonial eras. The beauty and natural history of this elegant species has been romanticized by many and perhaps nowhere more vividly than the enduring writings of Audubon.³ The wood duck is well-named for it is an obligate tree-cavity nester and at all times of the year inhabits forest or forest-

associated wetland habitats more than any other waterfowl. One of the most popular of game and market ducks, wood ducks were driven to near extinction in many parts of their eastern range during the late 19th century by uncontrolled forest clearing and market hunting. Concern for the species rallied broad public support, and protection provided under the Migratory Bird Treaty of 1918 set the stage for a remarkable recovery over the next several decades. Wood ducks are once again one of the most abundant of waterfowl in North America; they now sustain an annual sport harvest estimated at one million birds. This recovery of the wood duck is considered one of the major success stories of modern waterfowl management.

Within the Chesapeake Bay region, wood ducks use a wide variety of wetland habitats, from the smallest brooks

and pools in upland forest, extending downstream along riparian corridors, to marshes in tidal-fresh and the brackish reaches of estuaries. They are the most abundant of breeding waterfowl in the region with scattered pairs occurring throughout wetlands in association with deciduous forests. Greatest numbers of wood ducks occur in the region during fall migration in October and early November.

BACKGROUND

Taxonomy and Nomenclature

The wood duck is one of 15 species of waterfowl worldwide belonging to the perching duck tribe (family Anatidae, subfamily Anatinae, tribe Carinini) and the only perching duck endemic to North America.^{1,21} The wood duck is most similar in appearance and general biology to the mandarin duck of eastern Asia. Ornithologist Mark Catesby published the first description of the wood duck in his 1731 treatise entitled "The Natural History of Carolina, Florida, and the Bahama Islands".²⁵ Linnaeus classified and named the species *Anas sponsa* in 1758, and Friedrich Boie established the genus *Aix* in 1828.⁶³

Perching ducks are generally tropical and non-migratory; only the wood duck and its east Asian cousin, the mandarin duck, are migratory and north temperate in range.²¹ However, unlike other migratory waterfowl in North America, the wood duck is a permanent resident throughout much of its winter range and thus is the most abundant breeding anatid below about 40°N latitude. Because of this, the wood duck was commonly called the "summer duck" by early naturalists. Other common names include Carolina duck, acorn duck, swamp duck, tree duck, and squealer, a name derived from the distinctive alarm call of the female.⁵²

Morphology

From September through May, male wood ducks wear highly colorful and iridescent breeding plumage. Distinctive marks include striking bill coloration of red, white, and black; a bright vermillion eye and eye lid; a green iridescent head with prominent crest highlighted by two white stripes; a white throat with two white "finger marks" extending along the side of the head; a breast of rich burgundy terminated at a vertical white and black stripe in front of the wings; sides of bronze vermiculated in black; and a purplish-black iridescent back and large square tail.

Females, although generally drab, are more colorful than hen dabbling ducks. They have a gray-brown head and dark bill with a tear-shaped white patch highlighting dark brown eyes; their crest is wispy and sooty gray. Streaked breasts and mottled sides are rich chestnut to brown in color; bellies of adults of both sexes are white. Like other members of its tribe, wood ducks possess a goose-like bill,

sharp claws and perching ability, and a long tail for agile flight through trees.

At a distance, flying wood ducks appear black and can best be identified by their long, square tails, white bellies, and the characteristic "we-e-e-ek, we-e-e-ek" or squealing call of the female. Wood ducks also are prone to cock their heads in flight as if looking downward. Their wing beat is intermediate between that of the blue-winged teal and the mallard. On the water, wood ducks float higher than other ducks, with their large tails a distinguishing feature.

Among North American ducks, wood ducks are medium-sized with winter weights averaging about 700 g (1.5 lbs) for adult males and about 7% less for adult females (650 g or 1.4 lbs); immature wood ducks weigh about 3-4% less than adults.²²

Geographic Range

The range of the wood duck is confined almost entirely to the contiguous United States with some range extensions beyond the U.S. border (49°N latitude) into Southern Canada (see published range maps).^{7,41,60,61,65} As a rule, wood ducks are a freshwater species, potentially occupying all forest-associated wetlands to the limit of saltwater. Wood ducks are rare visitors to salt marshes or the seashore; however, they occasionally cross wide expanses of ocean to reach Newfoundland, Sable Island, Bermuda, and the Caribbean Islands.

Wood ducks generally are considered to have two distinct populations. The largest extends east of the Great Plains from east-central Saskatchewan to the maritime provinces, and south to central Texas, southern Florida, and Cuba. A smaller Pacific population exists from southern British Columbia and southwestern Alberta, south to central coastal California and the interior Sacramento and San Joaquin valleys. The eastern population generally winters in the deep South, primarily below 36°N latitude. The majority of the Pacific population winters in the Central Valley of California, especially the Butte Sink area north of Sacramento.^{7,60,61,65}

Distribution In the Chesapeake Bay

Wood ducks use a wide variety of freshwater wetland habitats, from the smallest brooks and pools of upland forest, extending downstream along riparian corridors to tidal-fresh marshes and the brackish reaches of estuaries. They make little use of habitats below the down-estuary salt tolerance of cattail.

During the day, wood ducks frequent woodland pools that provide rich sources of invertebrates in spring and an abundance of mast in fall. During brood rearing and fall migration, wood ducks make extensive use of estuarine river marshes along the Nanticoke, Patuxent, Elk, Chester,

Choptank, Blackwater, Transquaking, Chicamacomico, Wicomico, and Pocomoke Rivers.

Status

Clearly no one knows how abundant wood ducks were in the early 1800's and even today the reclusive nature of the species defies accurate field census. However, early writings indicate that the wood duck was exceedingly abundant all over the eastern U.S. and was common in game markets of the eastern seaboard by the early 19th century. It has been suggested that during the pristine period of the 19th century the wood duck might have been "the most abundant duck east of the Appalachian Mountains and, next to the mallard, the most abundant duck north of the coastal marshes of Louisiana in the Mississippi Flyway."¹⁰

The 19th century, however, brought great change to the status of the wood duck, especially in the post Civil War era. During this period, the need for lumber and open land for agriculture destroyed much prime wood duck habitat, especially old growth timber that provided prime nest sites. Increased hunting pressure to meet the demands of a growing game market also took its toll on wood duck populations. With hunting largely unregulated, wood ducks were taken at all times of the year, and were especially vulnerable to gunning because of their communal roosting habit. Knowledgeable hunters easily could take large numbers during morning and evening roost flights; in fall and winter such roosts might contain from several hundred to several thousand birds.

In market hunting areas of the east, the decline of the wood duck was apparent by the 1880's,⁶¹ and by the early 1900's many ornithologists were predicting extinction for the species.^{28,31} Biologist W. W. Cooke attributed the decline in waterfowl to "the constantly increasing numbers of sportsmen and market hunters, together with the invention of the breech-loading gun".¹⁶ Ornithologist A. K. Fischer pointed out the travesty of spring shooting and called for legislation to abolish this practice in all states in order to save the wood duck.²⁷

With establishment of the international Migratory Bird Treaty of 1916 and passage of the Federal Migratory Bird Treaty Act of 1918, wood ducks were given complete protection from illegal hunting, and in the 1920's and 1930's the species made a remarkable comeback. Although wood ducks were decimated in areas where market hunting was established, populations likely remained in many remote and inaccessible habitats, particularly in the South.⁹ Such areas probably served as important reservoirs for re-establishment. The advent of the nest box as a management tool in the 1930's also may have been an important factor in increasing wood ducks in local areas, particularly their widespread use after 1950.⁹

The wood duck population generally has continued to expand since the 1940's. Breeding Bird Survey trends show an estimated 120% increase in wood duck numbers in the eastern deciduous biome over the past 23 years (1966-1989), or 3.5% a year. In Maryland and Virginia, Breeding Bird Survey data indicate increases in wood duck numbers of about 2% a year during the 80's [unpublished data: USFWS Office of Migratory Bird Management (OMBM)]

Concurrent with this increase, a general decline in numbers of mallards and American black ducks has resulted in the wood duck occupying a more prominent position in the hunter's bag. The wood duck now ranks near the top of waterfowl harvested in most states in the East. Over the past 20 years, the estimated average U.S. harvest of wood ducks has been just over one million with 91% of that harvest occurring in the two eastern flyways (650,000 in the Mississippi and 339,000 in the Atlantic Flyway; unpublished data: OMBM).

In the Chesapeake Bay region, the wood duck harvest is only about 4% of this total. The estimated average annual harvest in the Bay region from 1978-1987 was 40,500 birds (Maryland and Virginia estimated annual state harvests of 8,500 and 32,000, respectively; unpublished data: OMBM). Biologist Frank Bellrose believes that the comeback of the wood duck relates directly to conservative management of its harvest; but he argues that the extensive loss of habitat, especially in the great interior bottomland forests, means that the species will never be as abundant as it was in the early 19th century.^{8,9}

LIFE HISTORY

Probably no other species of North American waterfowl has the capability of occupying as wide a range of habitat as wood ducks. Although greater numbers of wood ducks are found in large tracts of bottomland timber, they are remarkable in their ability to radiate into small upland water courses, woodland pools, and beaver flowages; they are the most adaptable of all waterfowl in their use of forested wetlands, especially those beneath a closed woodland canopy.

Throughout their range, wood ducks seek the security and solitude of sheltered backwaters, generally avoiding areas exposed to wind or current; they rarely are found far from forest, emergent, or near-shore cover. They have a particular affinity for close overhead woody cover as provided by a well developed forest understory or flooded timber with numerous snags and windfalls. They typically are associated with woody cover such as buttonbush, swamp privet, and willows.

Wood ducks are early migrants, and Northern birds begin southward movement soon after the first frosts in late

September and early October; only a few stragglers remain by November. Numbers of wood ducks increase steadily in the Chesapeake Bay in October and decrease sharply as birds move southward, usually by early November. In spring, some wood ducks reach northern nesting areas soon after ice-out in mid- to late March, although good numbers of birds are usually not present until April. Movement through the Chesapeake Bay region occurs with arrival of mild spring weather in late February and peaks during March.

Wood ducks are seasonally monogamous with courtship and pairing beginning in fall and continuing through winter. After arrival on the breeding ground, females spend considerable time searching for a suitable nest cavity. This activity is most intense in early morning as females and their mates are often seen perched high in trees inspecting potential nest sites. Egg laying begins as early as January 20 in the South,⁴⁴ but is delayed to April 15 at the northern limit of the range in New Brunswick.⁶² Nesting tapers off at all latitudes in June with only a few hatches extending into July in the north and August in the south.³⁴

A suitable tree cavity nest site is prerequisite to successful nesting and is the primary factor limiting the range of the wood duck to deciduous hardwood regions. The great abundance of wood ducks in pristine times is believed to be related in part to the abundance of suitable nest sites available in virgin old growth forest, especially within the interior bottomlands.

Generally, older, larger trees are the best cavity producers; trees less than 28 cm diameter at breast height (dbh) have few suitable nest cavities for wood ducks. Red and silver maple are particularly important cavity-producing species, but American elm, sycamore, ash, bald cypress, and others are locally important.

Wood ducks will nest in dead timber but prefer live trees with small entrances. Preferred cavities are those high in trees and in secondary limbs where they are better concealed from predation. Wood ducks have been known to use cavities as high as 65 ft (~20 m) above the ground.⁷ The ducklings exit the nest by free-falling to earth. Early naturalists and some subsequent reports¹² noted that wood ducks carried their young from such great heights. However, contemporary studies have not confirmed such behavior.

The average clutch size for the wood duck is 12 eggs, with a common range from 10-13.^{7,30,56} This is one of the largest clutch sizes for all North American ducks.⁴⁶ Although individual hens normally lay 15 or fewer eggs, larger clutches, sometimes of 30 or more eggs, are not uncommon in nest boxes. These large clutches are the result of more than one female laying in the same nest, a behavior

termed intraspecific nest parasitism, or more commonly, dump nesting.

Large clutch size and dump nesting are two characteristics that underlie the wood duck's high reproductive potential. Wood ducks also are known to have strong reneesting capability and are the only species of waterfowl in North America in which some females rear two broods in a single season.^{8,29,44,57} Second broods are not known north of Maryland, but are strictly a characteristic of southern wood ducks that invest little time and energy in migration and have a long nesting season.

Dump nesting is often a conspicuous feature of nesting wood ducks. It probably has evolved in response to competition for limited nest sites and because the wood duck is a highly social species that does not defend a territory during the breeding period. The frequency of dump nesting is most often associated with dense nesting or expanding populations.^{11,43} Dump nesting also is known to occur in response to nest predation³⁵ and may play an important role in the early nesting experience of females.³⁴

Because natural nesting populations are typically of low density, dump nesting usually involves a single parasitic female and results in a final clutch size of from 15-20 or more eggs. On average, such nests hatch with high success and contribute significantly to production. From available evidence, dump nesting is likely an adaptive and heritable behavior that enhances reproductive capability under natural nesting conditions. In contrast, dump nesting among dense box-nesting populations of wood ducks can be disruptive to nest success as a result of competition for limited nesting space. Under such circumstances, three or more females may lay in a single box, resulting in very large clutch sizes, high rates of nest abandonment, and poor hatchability.^{36,43}

Nest site availability is most frequently cited as the ultimate factor limiting numbers of wood ducks. So important is a suitable nest site that wood duck females show exceptionally high fidelity to nesting areas and even to specific nest sites.^{30,37,38} Females are likely to return to previous sites of successful nesting, provided the sites remain available.

Average brood survival for wood ducks is estimated at about 40%, with the greatest mortality occurring during the first two weeks after leaving the nest.^{4,55} Mortality frequently is associated with extended overland movements of young ducklings after departure from the nest.^{4,48} This finding underscores the importance of selecting a nest site near or over water and preferably near brood-rearing habitat that provides good food and cover. Brood survival is also weather-dependent, and especially so for newly hatched ducklings that are highly sensitive to chilling. During the peak hatching period, extended periods

of cold, wet weather are expected to increase exposure-related mortality among ducklings.

ECOLOGICAL ROLE

No other species of North American waterfowl uses forested wetlands as extensively as the wood duck. These habitats are used throughout the annual cycle for nesting, brood rearing, molting, roosting, migration, and wintering. Obligate cavity nesting is the wood duck's strongest ecological tie to old growth forest, whereas much of the food of the wood duck is intricately tied to the seasonal water dynamics of floodplain forest and associated wetlands. Availability of early spring aquatic invertebrates is especially critical in the nutrition of laying females.²⁴ Throughout most of their range, wood ducks have ecological ties to beaver that create forested wetlands,^{6,14,58} and woodpeckers, especially the pileated woodpecker, whose nest sites and numerous foraging excavations help create nest cavities for wood ducks.²⁰

Wood ducks and their eggs are prey for a number of birds, mammals, fish, and reptiles.⁵⁴ Important predators of adults and ducklings include the great horned owl, mink, raccoon, and red and gray foxes along upland edges. Aquatic predators include snapping turtles and predaceous fish such as northern pike and largemouth bass. Numerous nest predators exist but the raccoon is recognized as the most important throughout most of the wood duck's range.⁵⁴ The keen learning and climbing ability of this mammal has made it notorious as a nuisance predator of nest boxes.^{49,56} At northern latitudes, black and gray rat snakes are important predators of wood duck eggs and nestlings.^{5,13,26,32,33} Puncturing of eggs by starlings and woodpeckers (especially northern flickers) commonly has been observed in nest boxes;^{54,68} however, little is known of the extent of this activity at tree-cavity nest sites.

With a strong, goose-like bill and a large nail for grasping food items, the wood duck might best be categorized as a browser or picker, rather than a grazer (like geese) or dabbler (like the broad-billed dabbling ducks). Wood ducks are shallow-water feeders obtaining their food primarily on or near the surface of the water; their optimum water depth is 8-45 cm.⁵⁴ Wood ducks seem more prone to simply immerse their heads and necks rather than tip up to feed like dabbling ducks.⁶¹ In fall, wood ducks are also prone to go ashore or fly into wooded areas in search of acorns or other mast, and they are known to forage on waste grains, such as soybeans, corn, and wheat in agricultural fields adjacent to good wetland cover.

Over an annual cycle, wood ducks feed on a variety of foods to satisfy energetic and nutritional needs. Many of these foods may be only seasonally or regionally available, and thus wood ducks might be expected to consume a wide variety of foods from a diversity of habitats at

different times of the year. Much of the food comes from aquatic habitats associated with flooded bottomlands and swamps, and the quiet backwaters of wooded ponds, streams, and marshes. As might be expected, wood ducks feed more than any other waterfowl on the fruits of woodland plants and mast from the forest.

Like most waterfowl, wood ducks are decidedly vegetarian during the nonbreeding period and consume a wide variety of seasonally available plant foods including duckweeds, seeds of sedges, grasses, waterlilies, and smartweeds, as well as submerged plants such as pondweeds and wildcelery.^{50,51} Acorns are the outstanding fall food of wood ducks throughout their range.^{2,19,22,47,50,53,67} Other excellent fall foods include seeds of wild rice,^{19,51} burreeds,^{18,19,67} and the fruits of arrow-aram.^{15,50} Additional forest mast consumed by wood ducks includes galls and cones of bald cypress, beech nuts, seeds of sweet gum, water hickory, and the drupes of black cherry.^{47,50,53} Animal foods consumed by wood ducks include a variety of aquatic insect life, especially odonates (dragonflies and damselflies), hemipterans (bugs), coleopterans (beetles) and dipterans (flies), as well as snails, crustaceans, fishes, and amphibians.⁵⁰

Female wood ducks shift their diets to a higher percentage of animal foods during the breeding period.^{24,47} In addition to a variety of aquatic invertebrates, mostly insects, they often consume a significant portion of terrestrial insect life that is either inadvertently blown into the water, or gleaned from emergent vegetation along the shoreline.⁴⁷ Ducklings also are known to consume a high percentage of animal foods, primarily insects, during the first two weeks of life to meet the protein demands of rapid growth.^{39,42}

In the Chesapeake Bay region, wood ducks examined from the Patuxent River bottomlands consumed primarily beech nuts and acorns of white and pin oak, the seeds of halberdleaf tearthumb, hornbeam, and black gum, and the leaves of the submerged plants ribbonleaf pondweed and Nuttall waterweed. From estuarine river marshes, wood ducks consumed predominantly the fruits of arrow-aram, along with a variety of other seeds generally from large-seeded marsh plants, such as burreed and halberdleaf tearthumb.⁶⁶

HABITAT REQUIREMENTS

Wood ducks use a variety of wetland habitats to meet their daily and seasonal life requirements. Food, cover, and water govern the distribution of wood ducks throughout the year, with nest cavities playing an important additional role during the nesting period. During the annual cycle, specific habitat requirements can be identified for such events as breeding, brood rearing, molting, roosting, and migration.

Breeding Habitat

Important breeding areas for wood ducks satisfy three specific needs: (1) good foraging habitat that provides adequate nutrition for egg laying, (2) large deciduous trees that provide suitable tree-cavity nest sites, and (3) daily roosting habitat.

Seasonally flooded bottomland hardwood forest is generally considered the most attractive breeding habitat for wood ducks because it potentially satisfies all three needs for successful nesting. Especially important foraging habitats within bottomland hardwoods are shallow, ephemeral, "vernal" pools that harbor abundant, early-spring invertebrate. A mosaic of such pools may form within poorly drained bottomlands from snowmelt and spring rain, or from receding floodwaters.

Many other wetland types also provide food for breeding wood ducks, such as shrub swamps, the emergent or flooded shrub fringes of forests, lakes, ponds, rivers, marshes, and flooded dead timber areas with interspersed shrub or other woody cover. Newly flooded forest, such as created by beaver, is particularly attractive to wood ducks because of its excellent cover and productivity.

Wood ducks will search throughout flooded forest for suitable nest cavities. If such sites are in short supply, they may move a considerable distance in bordering upland forest, usually searching along small water courses or canopy openings within short distances from permanent water. Wood ducks usually do not penetrate upland forest farther than 0.5 km in search of nest cavities.

Brood Rearing Habitat

By the time most broods hatch in late spring, water generally has retreated in seasonally flooded bottomlands and leaves have closed the forest canopy. Remaining watered areas provide adequate cover for broods, but without sunlight such sites have little productivity and therefore little food for ducklings. Broods therefore seek more permanent marsh and shrub swamp habitats where aquatic productivity is high and cover is readily available. A general pattern is for broods to migrate downstream along water courses from scattered upland nest sites and aggregate in relatively large, permanent marsh habitats.

A variety of wetland types provide brood-rearing habitat for wood ducks. Common characteristics of these sites are water permanence and interspersed of deciduous woody and herbaceous vegetation. The shrub layer provides the cover and security for broods and the emergent and submergent aquatic vegetation harbor the invertebrate food species. Quality brood-rearing habitat has been described as a patchy network of emergent cover composed of downed timber, deciduous woody and herbaceous plants, interspersed with a network of waterways. Ideal cover composition has been suggested as 30-50% shrubs,

40-70% herbaceous emergents, and 0-10% trees; the optimum ratio of cover to open water has been suggested as three to one.⁵⁴

Roosting Habitat

As young birds become flighted in late summer, they begin aggregating on roosts; their numbers increase through fall. Roost habitats are especially important in providing protection for large numbers of birds, sometimes in the thousands. Roost sites may be in small outlying wetlands that otherwise get little use during the day. Such sites are always characterized by extensive woody cover, as typically provided by shrub swamps of button-bush, willow, or swamp privet, interspersed with channels of open water and herbaceous vegetation. In early spring, flooded bottomland forests with well developed understories of saplings or windfalls, commonly are used for roosting. Although wood ducks remain gregarious throughout the year, communal roosting is best-developed in late summer and fall. It is at this time of the year that the most important roost sites can be identified.

Molting Habitat

Because wood ducks become flightless for four to six weeks during the post-nuptial molt, they seek refuge in large, permanent wetlands with extensive cover and abundant food resources. Extensive emergent marshes of many types may be used, but again, woody overhead cover is a preferred characteristic. In any given area, usually the most extensive emergent marsh or shrub swamp is most heavily used by molting birds.

Migration Habitat

Flooded hardwood bottomlands and riparian corridors are the primary fall and spring migration habitats of wood ducks. Such areas are used heavily because of the ready availability of acorns and other mast in fall and a combination of persistent overwinter plant and high invertebrate availability in spring. River marshes provide an abundance of preferred foods, such as seeds of wild rice, smartweeds and burreed, are also important foraging areas.

SPECIAL PROBLEMS

Habitat Degradation

Because wood ducks potentially make use of all types of forested or forest-associated wetlands, including the smallest woodland pools and brooks, they occupy habitats that frequently are affected by development, especially along the Bay's heavily populated western shore and in the Baltimore-Washington corridor. In more rural environments, such as southern Maryland or the Eastern Shore, clearing of forest for agricultural use in proximity to water courses destroys potential wood duck habitat and in most cases jeopardizes the integrity of adjoining or downstream wetlands through extensive siltation and altered hydro-

ogy. Because wood ducks occur in sparse numbers over much of this habitat, the degradation of any one habitat may be negligible at the local population level, but cumulative losses may be significant. Habitats worthy of special protection are the hardwood floodplain forests adjoining and especially upstream from large marshes.

Timber Management Practices

Management of timber stands along riparian corridors and extending along the smallest streams and brooks is a primary concern to sound wood duck management. Harvest of timber at the earliest merchantable stage effectively eliminates overmature and old-growth timber that contain the best nest cavities for wood ducks and provide good mast production. Conversion of forest stands to monocultures of pine precludes the use of such areas by wood ducks.

Siltation

Excessive siltation is characteristic of many of the tributaries of the Chesapeake Bay. Caused primarily by erosion associated with land clearing for development and runoff from agricultural land, siltation can smother aquatic life including benthic fauna and submerged aquatic vegetation, and can accelerate the loss of extensive emergent marshes that are important to wood ducks.

Channelization

The dredging of small streams and tributaries and bank stabilization practices that destroy overhanging cover, produce excessive depths, current, or hard bottoms, and are particularly destructive to natural wood duck habitat. These practices destroy the quality of shallow-water foraging sites and the cover desired by wood ducks. In addition, channelization of larger rivers, especially in concert with damming for flood control, can alter the natural seasonal flooding pattern within bottomland forests that is intricately tied to the maintenance and productivity of wood duck breeding and foraging habitat.

Contaminants

There is little information on wood duck exposure to environmental contaminants, or their effects, in the Chesapeake Bay region. Wood ducks do, however, occupy small water drainages that often receive water directly from agricultural land, urban runoff, effluent from sewage plants, and wastes from industrial plants. They therefore have potential exposure to contaminants either directly or through the food chain.

Wood ducks also have been known to suffer losses due to ingestion of spent lead shot. However, with full implementation of steel shot regulations by the U.S. Fish and Wildlife Service in 1991, lead poisoning should markedly diminish as a threat to wood ducks or other North American waterfowl.

Several metals have been detected in wintering Chesapeake Bay wood ducks from collections made in primarily freshwater marshes.²³ Metal concentrations, except for lead, in wood ducks were lower than, or comparable to, those found in other ducks. The median dry weight concentrations of cadmium, lead, zinc, and copper in liver tissue were 0.39, 3.8, 151, and 15.3 mg kg⁻¹, respectively. Lead burdens were considered high enough to produce sublethal effects, and probably were caused by ingestion of spent lead shot. A recent review of contaminants in birds of the Chesapeake Bay, found no additional information related to wood ducks.⁵⁹ For further information on toxic contaminants see EFFECTS OF CONTAMINANTS ON BIRDS (this volume).

RECOMMENDATIONS

Structural Habitat

Habitat management should be designed to protect and enhance key habitats throughout the wood duck's annual cycle. Most important are the protection of riparian corridors and the management of contiguous bottomland floodplain timber stands, but valuable wood duck habitat extends throughout the watershed to include all stream, marsh, and bordering forest. Protection of primary fall roost sites is also important, especially those used by large numbers of migrants. Management of wood ducks also includes creation of new habitats and use of nest boxes where appropriate. Wood ducks respond well to creation of small lakes, ponds, or impoundments in wooded areas, such as those fostered by progressive beaver management; in favorable habitats, wood ducks usually respond well to nest box management. Green-tree impoundments have also been successfully managed in the south and mid-west and can produce attractive habitat for wood ducks during fall and winter.^{40,64}

Water Quality

Any actions that will improve water quality, i.e. reduce nutrient loads, silt loads and sedimentation rates, biological oxygen demand, or toxic substances within the watersheds of the Chesapeake Bay, will benefit aquatic habitats for wood ducks. See AMERICAN BLACK DUCK: **Recommendations** (this volume) for a list of beneficial actions.

Management of Riparian Corridors

Conservation of wetlands (by avoiding drainage, filling, or contamination) and riparian forests, including those along the smallest watercourses, will protect the most important wood duck habitats, including the smallest wetlands used by wood ducks. Protection of natural forested buffer zones along all water courses will benefit wood ducks. Of special value are the large, contiguous, floodplain forests, more especially those that flood seasonally. Timber harvests should be managed carefully within these forests and along riparian buffer zones to foster development of mature and old growth stands,

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particularly those containing mast-bearing and cavity-producing tree species. Natural hydrology should be maintained within tidal and nontidal wetlands and floodplain forests. Channelization is particularly destructive of wood duck habitat and should be avoided.

Harvest Management

The near-extinction of wood ducks in many parts of their eastern range near the turn of the century has taught several lessons: (1) that wood ducks are highly vulnerable to gunning; (2) that local populations may be easily overharvested; and (3) that wood ducks are exceptionally slow to pioneer and repopulate areas where they have been eliminated. Prudent management requires conservative harvests to provide for an abundance of wood ducks in the future.

CONCLUSIONS

The Chesapeake Bay is an important region for migrating and breeding wood ducks, but harbors few birds in winter. Because they have been protected from overhunting by federal legislation passed in the early 20th century, wood ducks have made a remarkable comeback from their once-decimated numbers. Their numbers can be maintained, and further increased in the Bay by management practices that carefully protect their woodland habitats.

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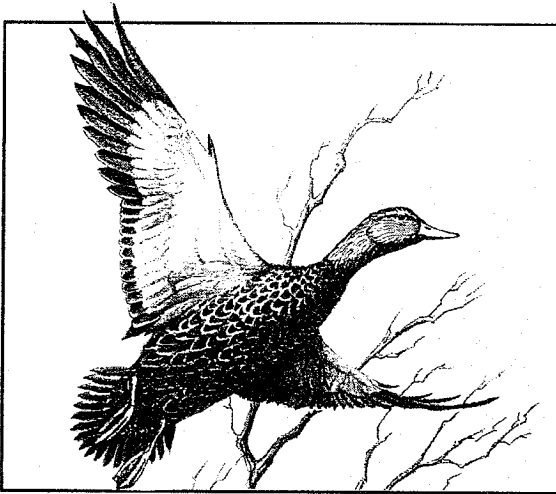
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AMERICAN BLACK DUCK

Anas rubripes

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breeding and sanctuary wetlands, and continuing conservative hunting regulations.

The American black duck is a species of concern both in Chesapeake Bay and continentally because of a long term decline in population numbers since the 1950's. The Chesapeake Bay is an important area to black ducks because they breed, migrate through, and winter there. It is probable that at one time, a significant proportion of the continental population of black ducks were produced in the Chesapeake Bay region. Habitat degradation, through erosion, development, and eutrophication, is a primary cause for the reduction in numbers of black ducks produced on the Bay. Another problem for the remaining black ducks may be the release of hand-reared mallards into the wild. The production and wintering conditions for black ducks on the Bay can be improved with a more active habitat management program aimed at increasing the abundance of submerged aquatic vegetation, protecting existing

INTRODUCTION

American black ducks have always been a visible component of the avifauna on Chesapeake Bay. Numbers of black ducks wintering on the Bay have declined markedly from the highs of the 1950's [200,000; unpublished data: USFWS Office of Migratory Bird Management (OMBM)] to the present levels of around 32,000. This decline has leveled off since harvest restrictions were implemented in 1983; however, numbers of breeding black duck are continuing to decline in Maryland, based on the Breeding Bird Atlas [unpublished data: J. Sauer, U.S. Fish and Wildlife Service (USFWS)]. Evidence of declines in annual survival rates of black ducks since the 1950's are not well documented; generally annual survival rates appear stable.²⁸ The long term decline in population numbers may be the result of reproduction not keeping pace with annual mortality.

Reasons for production problems might include loss of nesting habitat, reduced fecundity of adults, and lower survival of young before fledging. Widespread changes in

habitat both in the far north and in the Chesapeake Bay region have occurred since the 1950's.^{9,26} The available evidence is less clear for the far north, but it is clear that in the Chesapeake Bay region, much less habitat is available today for nesting and for rearing broods.⁴⁵ This long term decline in black duck population trends has been more consistent than that of other regional waterfowl; there are fewer short term positive deviations in yearly population than for other waterfowl. Below, I examine the life history and factors thought to influence population dynamics of black ducks in an attempt to understand the population trends and management programs that could alleviate them.

BACKGROUND

A complete description of black duck morphology may be found in Palmer.³⁶ The black duck is one of several monomorphic species of North American ducks. Both sexes are sooty-brown with bluish-purple speculums bordered by black which is sometimes bordered with white on the trailing edge. The head is somewhat paler than the

body. In flight, the white underwings contrast sharply with the brown-black body. Black ducks resemble mallards in body size (~53 cm long, ~25 cm wingspan) and mass (~1200 g). Hybrids with wide variation in plumage patterns occur between black ducks and mallards. Frequency of occurrence of hybrids varies regionally.³⁶

Some ornithologists recently have questioned the black duck's status as a species separate from the mallard² while others have defended its separate status.^{22,31} The American Ornithologists' Union has not voted on the matter, so for now the black duck remains a distinct species from the mallard.¹

Primarily a species of eastern North America, the black duck is found east of the Great Plains and south of the tundra. The breeding range extends from northeastern Manitoba to Newfoundland and south to the southern Great Lakes region. The Atlantic Coast breeding range extends south to coastal North Carolina. Highest densities of nesting black ducks are thought to occur along the Great Lakes, St. Lawrence and Acadian areas.³⁷ Extremely high densities of nesting black ducks occur locally in Chesapeake Bay.^{45,46}

Migration corridors are primarily along the Atlantic Coast with another corridor along the Mississippi River Valley. Substantial overlap between breeding and wintering ranges makes it difficult to delineate well-defined migration corridors. Black ducks winter from the St. Lawrence lowlands to the Gulf Coast. Most of the migratory black ducks along the Atlantic Coast winter between Cape Cod and Chesapeake Bay,⁴² making the Bay an important breeding and wintering region for the continental black duck population. Some subpopulations of black ducks, such as those in the St. Lawrence and the Chesapeake Bay, may be non-migratory.^{18,24}

The black duck and the canvasback epitomize Chesapeake Bay more than most other duck species. Unlike the canvasback which is easily observed by the birdwatcher, the black duck is wary of humans⁴⁹ and thus difficult to observe. Exceptions occur on National Wildlife Refuges such as Eastern Neck or Blackwater where black ducks are readily visible and less wary. At one time the black was the number one puddle duck in the Atlantic Flyway hunter's bag and in hunting lore.^{48,49} In recent years it has dropped to the number three bird in the Atlantic Flyway bag, comprising only 10% of the total duck harvest.⁴⁷ The black duck harvest has fluctuated around 15,000 in Maryland and 12,000 in Virginia (unpublished data: OMBM). In addition to being important to the Chesapeake Bay region, the black duck is also of national importance, as signified by the North American Waterfowl Management Plan.⁶

The long term decline in black duck numbers has led to harvest restrictions in bag limits and season lengths. Restrictions, developed to reduce harvest by a minimum of 25% of the 1977-81 average harvest, began during the 1983-84 hunting season and remain in effect today. Despite considerable reductions in the estimated recovery rates and total harvest of black ducks (e.g., ~50% reduction in harvest in Maryland compared to the average kill during 1977-81), population numbers remain low. Over the short term, however, population numbers have stabilized, providing the first ray of hope in the black duck picture since the mid-1950's. Current harvest restrictions are expected to continue.

LIFE HISTORY

Black ducks are among the earliest-pairing puddle ducks.³⁶ Courtship activities in the Chesapeake Bay region can begin as early as September, and by December most pair-bonds are formed.⁴⁶ Males remain with their females for about two weeks after egg-laying, and then desert the females.⁴⁵

Nesting

Nesting occurs throughout the Chesapeake Bay area with the greatest densities thought to occur on the Eastern Shore of Maryland from the Chester River south to the Crisfield area (Map Appendix). Because of the black duck's aversion to human disturbance,^{10,15} most black ducks now nest on uninhabited islands or remote marshlands and adjacent uplands. During the mid-1950's Stotts and Davis⁴⁶ found 593 black duck nests in the Chesapeake Bay region, of which 65% were in upland areas, 17% in marshes, and 19% in offshore duck blinds. Today, few offshore duckblinds are available, so they no longer comprise a significant part of the nesting habitat.⁴⁵

Nesting begins quite early in the Chesapeake Bay region, about mid-March, and continues until early August.⁴⁶ The amount of renesting varies with the weather⁴⁶ (unpublished data: D. Krementz, USFWS). In years with cold late springs, renesting can be common. In years with warmer drier weather, nesting is more synchronized and renesting less common. Clutch size varies from 6-12 eggs and declines from the onset of laying through the nesting season. Flooding causes some nest loss, especially in early season nests.

Migration

Migration into Chesapeake Bay begins in late September and peaks in October-November.⁴³ Most of the Bay's migrant black ducks originate in Quebec and Labrador,¹⁸ but we do not know how many of those wintering in the Bay are derived locally or are migrants from northern areas. Spring migration begins in mid-February and peaks

in early March.⁴³ The destination of migrating post-breeding ducks is not well documented.

During the 1950's, a large portion (~20%) of the continental black duck population wintered on Chesapeake Bay.⁴³ For example, during 1955, an estimated 224,000 black ducks used the Maryland portion of the Bay compared to 24,000 ducks during 1989 (unpublished data: OMBM). The primary wintering area for the Atlantic Flyway population of the black duck has shifted from the Chesapeake Bay to the New Jersey coast where almost 90,000 black ducks were counted in 1989. This shift in wintering areas has important management implications because recent studies indicate that black ducks are faithful to wintering areas after spending a winter there.^{13,14} The shift in wintering areas may have resulted from a combination of lower survival rates of black ducks wintering on Chesapeake Bay relative to those on the New Jersey coast and the fact that winter habitat conditions along the New Jersey coast are preferable to those in the Bay. While in the Bay area, black ducks can be found throughout the region, especially along the lower Eastern Shore in Maryland and the Western Shore in Virginia (Map Appendix). The Chesapeake Bay region has been, and with improved habitat quality can be again, an important wintering area for the continental population of the black duck.

ECOLOGICAL ROLE

Mallards have moved eastward into black duck habitat since the early 1900's.²⁵ This change in distribution of the mallard, and concomitant decline in numbers of black ducks, has led some biologists to speculate that mallards play a role in reducing the black duck population because of hybridization and competition for limited space and resources.^{2,12,45} Although there is evidence of increasing numbers of mallard-black duck hybrids in the hunter's bag,³⁰ the mechanisms responsible for these hybridizations remain unclear.^{2,5,9,22,30} Competition for space and resources between mallards and black ducks is poorly understood. What little work has been conducted on this subject^{10,23,45} has not established whether changes in numbers of mallards and black ducks are the result of cause and effect or merely a correlation with other coincident factors. Thus, at this time, we cannot speculate on whether mallards are directly competing for limited resources with black ducks.

Predation rates in black duck nests are usually high, with the fish crow and American crow leading the list of predators. In mainland nesting situations, mammalian predators such as red fox and raccoons are predominant sources of nest loss. Predation rates on broods also can be high (unpublished data: D.G. Krementz, USFWS). Predators include snapping turtles, black rat snakes, great horned owls, bald eagles, and red fox. Inclement weather

also can take a heavy toll of young, especially when the brood is less than one week old.

Because of the wide variety of habitats used, black duck food habits are diverse. Generally, black ducks are thought to consume more animal foods than most puddle ducks, especially when they use brackish or saltwater marshes.³ A sample of 212 black ducks collected from a variety of habitats in Maryland during the fall and winter of the late 1950's⁴³ documented the varied food preferences of black ducks. In freshwater marshes, black ducks eat twigrush and olney bulrush seeds, and fish. If agricultural fields are nearby, black ducks use agricultural crops, especially corn. In bottomland hardwoods, the principal foods are beechnuts and oak acorns, seeds of hornbeam, and snails. In estuarine river marshes, black ducks consume seeds of dotted smartweed, halberdleaf tearthumb, pickerelweed, arrowleaf tearthumb, wild rice, burreed, giant burreed, and arrow-arum. In brackish marshes and estuarine bays, black ducks consume redhead grass seeds, leaves, stems, and rootstalks; olney bulrush seeds; widgeon grass seeds, stems, rootstalks, and leaves; eelgrass stems and leaves; saltmarsh snails; baltic clams; and fish. In saltmarsh habitats, black ducks forage on fish (mostly Poeciliidae), saltmarsh snails, ribbed mussels, and widgeon grass seeds, stems, rootstalks, and leaves.

These surveys were conducted during the 1950's when submerged aquatic vegetation (SAV) was more plentiful. A recent analysis of black duck food habits³³ indicated that of eight food items monitored, two food items (twigrush and olney bulrush) have become less important, supposedly because of reduced availability, whereas one food item, dotted smartweed, has become more important.

HABITAT REQUIREMENTS

Structural Habitat Requirements

Because they breed, migrate through, and winter in the region, black ducks use a wide variety of habitat types in Chesapeake Bay; each activity involves slightly different habitat requirements. Stewart⁴³ described in depth 13 habitat types found in the upper Chesapeake Bay region in the mid- to late 1950's, when the black duck population reached its all time peak.³⁹ These habitats may be a valuable standard which today's habitat management should strive to re-create.

Nesting

In upland areas, nests usually are associated with both coniferous and deciduous overstories and dense understories of common poison ivy, honeysuckle, brush, or grasses. Fresh, brackish, and salt marshes are also used for nesting. Nests in marshes are often associated with shrubs but may be in monotonous stands of sedges, rushes, or grasses.

Brood Rearing

The female leads her brood away from the nest shortly after hatching (< 48 h), usually to the nearest brood-rearing marsh. Typically, brood-rearing marshes in Chesapeake Bay consist of broken saltmeadow cordgrass interspersed with needle rush or olney bulrush. These marshes often are bordered with common reed, saltmarsh cordgrass and high tide bush. Lack of suitable brood-rearing marshes increases brood loss (unpublished data: D.G. Kremetz, USFWS).

SPECIAL PROBLEMS**Declining Food Resources**

Munro and Perry³³ addressed the relationship between black duck numbers wintering in the Chesapeake Bay and loss of SAV. They found that black duck numbers were related significantly to the abundance of SAV in the Chester River area and to a lesser degree in other areas such as the Honga River and Bloodworth-Smith Island areas. Thus, declines in SAV abundance appear to correlate with declines in local black duck populations.

The Potomac River is a more dramatic example of how SAV can influence winter distribution and abundance of black ducks. According to the mid-winter index (unpublished data: OMBM), the winter abundance of black ducks recently has increased sharply in the upper Potomac River basin, coincident with the introduction of *Hydrilla*. Although the black duck's actual dependence on this plant as a food source is unknown, it is thought that many invertebrates valuable to the black duck thrive in *Hydrilla* (Personal communication: M. Perry, USFWS). This plant also promotes re-establishment of other beneficial SAV.⁷ See SUBMERGED AQUATIC VEGETATION, this volume, for SAV water quality guidelines.

Winter Feeding

Feeding of corn to wintering waterfowl along the Chesapeake Bay waterfront has become a popular hobby for many bayfront residents, resulting in a significant amount of corn fed to ducks on a daily basis (personal communication: G.M. Haramis, USFWS). Black ducks and especially mallards use this resource. Its impact on black ducks is unknown, but it conceivably could influence winter distribution, survival rates, and exposure to disease. This recent phenomenon should be investigated as to its role in Chesapeake Bay waterfowl management.

Disturbance

Black ducks always have been and continue to be very wary of humans.^{10,15} Development along the Chesapeake Bay shoreline increased dramatically during the 1970's and 1980's and is predicted to continue.¹¹ Human-related disturbances affecting black ducks include dredging, shoreline erosion control, marina developments, housing, channelization, and marshland filling and draining.

Recreational activities such as hunting, fishing, and pleasure boating could also adversely affect black ducks. Repeated disturbance markedly affects black duck habitat selection and use during the winter period.^{8,15,32} Disturbance of nesting ducks is also deleterious, including egg-collecting by humans.^{10,46,45}

Toxics

Despite the presence of both metal and organochlorine pollutants in the Bay, there are no suspected problems from these pollutants in Chesapeake Bay black ducks, apart from lead shot poisoning³⁵ (personal communication: G. Heinz, USFWS). Recently, acid rain has been touted as possibly affecting black duck productivity.²⁰ Work by Haramis and Chu²¹ in experimentally acidified wetlands in the Chesapeake Bay area demonstrated that acid rain can lead to reduced growth rates and lower survival rates of black ducks. The effects of acid rain on black duck productivity in the Bay are unknown. Finally, excessive nutrient loading is thought to be a predominant factor in the decline of SAV populations in the Bay area.⁴¹ Without SAV, black ducks will be forced to use other food resources or simply not remain in the area. EFFECTS OF CONTAMINANTS ON BIRDS this volume, provides more information on this subject.

Mallards

A cause for concern in Maryland is the release of hand-reared mallards into the wild for sport-shooting. Between 1974 and 1989, for example, the Maryland Department of Natural Resources (personal communication: L. Hindman, MDNR) released about 285,000 mallards into the wild. In addition, private programs release thousands of mallards with the result that the total number of mallards released presently exceeds 150,000 annually (personal communication: L. Hindman, MDNR). Although the survival rate of these released mallards is not well documented,⁴⁰ enough mallards are released annually to compete for limited resources with black ducks and to threaten the black duck gene pool through hybridization.^{2,45}

Hunting

Although the effects of hunting on the continental population of black ducks are not well understood,^{4,16,19,29,34} there is little question that on a local scale, hunting can have a significant impact on black duck populations.^{29,38} This effect supposedly results from young or naive birds being exposed to the intense hunting pressure of the first weekend of the hunting season.^{27,44} Since Chesapeake Bay has a resident population of black ducks, these ducks are, likewise, susceptible to overharvest.

A recent phenomenon worth mentioning in regards to the effects of hunting is the registered shooting area (RSA). These operations release and feed hand-reared mallards, and allow hunters to shoot legally both hand-reared and wild mallards on designated lands. These areas have the

potential to attract and hold black ducks. Under these artificial situations, unnatural concentrations of ducks conceivably could increase the chances of disease outbreak,¹⁷ alter winter distributions, or increase the reliance of black ducks on cereal grains. The ramifications of RSA on black ducks in the Chesapeake Bay region are not understood and should be investigated.

RECOMMENDATIONS

Harvest Regulations

Breeding populations of black ducks must be protected through harvest regulations. The current harvest regulations in Maryland are an example of a viable means of addressing this issue (i.e., closure until the second part of the split season and, when the season opens, a one black duck per day bag limit). Regulations implemented in the Bay since the early 1980's, including reduced bag limits, shortened seasons, and a retarded opening day for black ducks, have markedly reduced both harvest and harvest rate in the region (unpublished data: OMBM).

Disturbance

Because black ducks are very wary of humans, sanctuary is needed, especially during periods of high mortality (e.g., hunting season) and during the breeding season. Presently three National Wildlife Refuges (NWR) exist in the heart of the traditional black duck range in the Chesapeake Bay: Eastern Neck, Blackwater and Martin NWR. Expansion of these refuges, or creation of new refuges, could benefit both wintering and nesting black ducks. Nesting black ducks would benefit most by strict protection of nesting islands from all trespassing, during the nesting season. Additionally, brood-rearing black ducks would greatly benefit from more access to brood rearing marshes located in close proximity to one another. Creation of non-toxic dredge-spoil islands with both upland and marshland habitats also might assist breeding black ducks, especially if these islands were off limits to people during the breeding season.

Habitat Management

Management of public and private wetlands and adjacent uplands for black ducks is needed. Currently, Blackwater NWR has implemented a number of management prac-

tices which could be used to the benefit of black ducks elsewhere in Chesapeake Bay. Management practices there include moist-soil management of impoundments for invertebrate production, periodic burning of *Scirpus* marshes for seed production and rejuvenation, and trapping programs for targeted predator species. These programs serve two functions. First, they directly enhance breeding and wintering black duck habitat, and secondly, they serve as models to guide private landowners in managing their own lands. Private landowners are an overlooked resource in the management of land for black ducks in the Bay region.

Water Quality

In addition to better wetland and upland land management, improved water quality in the Bay will also help black ducks. Helpful steps include: better control of stormwater runoff, implementing agricultural practices which reduce wind and water soil erosion (e.g. shelter belts, no till and low-input farming), better stormwater management on construction sites, and improved wastewater technologies. The resurgence of *Hydrilla* in the fresh-tidal Potomac River, probably as a result of improved water quality, has done much to attract and hold black ducks there. Similar improvements in water quality in the Chesapeake Bay also would aid in recovery of SAV. Without an improved food base, it will be difficult to attract, hold, or produce more black ducks.

CONCLUSIONS

The continental population of the black duck has declined across its entire range since the 1950's, although recently, the population appears to be stabilizing. Many factors are responsible for this decline, including overharvest, loss of habitat, pollution, and hybridization and competition with the mallard. If the population goal of the North American Waterfowl Management Plan of 385,000 black ducks by the year 2000 is to be achieved, implementation of the above recommendations will be necessary.

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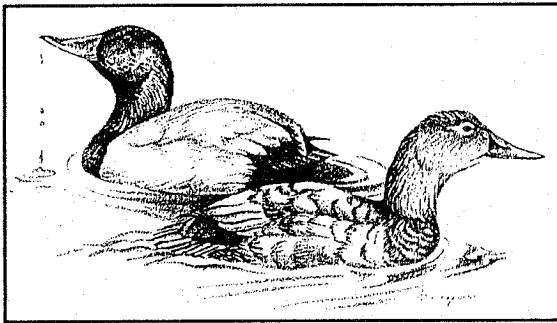
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CANVASBACK

Aythya valisineria

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to hunting - degradation of Chesapeake Bay, the species' primary wintering area, probably also has played a significant role.

Changes in the Bay significantly affecting the canvasback include increased nutrients, sedimentation, turbidity, and other contamination of the aquatic environment that has led to major changes in foods available. The most important change has been the drastic decline in submerged aquatic vegetation (SAV), the historic and preferred food of canvasbacks. Presently, a few species of edible-sized clams, primarily the Baltic clam, are critical to maintaining the wintering canvasback population. Although the effect of the dietary change is not fully understood, it suggests a declining habitat quality that could affect canvasback winter survival, winter distribution, and subsequent breeding performance. Further degradation of the Bay is likely to lead to a further decline in canvasback use.

The Chesapeake Bay remains an important wintering area for canvasbacks, and restoration of the Bay is critical to restoring the continental canvasback population. Restoration of water quality is fundamental to improving the abundance and diversity of foods available to canvasbacks, especially SAV.

INTRODUCTION

During the period of colonial settlement in North America, Chesapeake Bay displayed the greatest spectacle of wintering waterfowl yet witnessed on the continent. The highly productive shoal-water habitats and the diversity of foods they harbored attracted countless thousands of ducks, geese, and swans arriving from the interior of a yet unexplored continent. Most impressive of all waterfowl was the canvasback, a large, fast-flying diving duck that amassed in enormous flocks. The species was attracted to lush beds of wildcelery and other native aquatic plants that abounded in the expansive shallow waters of the Bay.

The pioneer American ornithologist Alexander Wilson (ca. 1800) described wildcelery as so abundant in the Bay that "a boat with difficulty could be rowed through it, it so impedes the oars. The shores are lined with large quantities of it, torn up by the ducks, and drifted up by the winds, lying, like hay, in windrows."⁶⁶

Because of its great numbers, large size, and excellent eating quality, the canvasback became prized food throughout the region; by the late 19th century it was the most famous and esteemed of all American waterfowl. The canvasback's popularity earned it top price in the game markets of the post-Civil War era. As a result, the

canvasback became more and more heavily hunted. Nowhere was the canvasback more persecuted than in Chesapeake Bay where large flocks were assailed with every contrivance. Large-bore shotguns and sink-box blinds gave way to boat-mounted batteries of cannon and punt guns used to kill birds en masse, even at night. This unregulated harvest ended with passage of the Migratory Bird Treaty Act of 1918 that empowered the Federal Government to set seasons and bag limits on the hunting of migratory game birds.

As the new law abruptly ended the game markets, canvasbacks escaped wanton overharvest, but in time they faced new threats from encroaching civilization on their breeding, migration, and wintering habitats. By the mid-20th century, the spread of grain agriculture had significantly reduced and altered prairie breeding habitats. During the same period, expanding human populations in the East were placing ever greater stress on the Chesapeake Bay.

Today exploitation and pollution of Chesapeake Bay has led to major decline of one of the world's great natural systems. For canvasbacks and other Bay waterfowl, the loss of SAV has been the greatest single setback. Fortunately Bay canvasbacks have been able to switch to alternate foods, mainly shellfish, and remain in generally good numbers. Other species, such as redheads and American widgeon, have all but abandoned the Bay. If we wish to restore the Bay canvasback population, we must restore SAV. Further decline of the Bay will only lead to further decline in numbers of canvasbacks.

BACKGROUND

Taxonomy and Nomenclature

The canvasback is one of 35 indigenous species of North American ducks (family Anatidae, subfamily Anatinae) and the largest of 14 closely related diving ducks worldwide belonging to tribe Aythyini^{2,19}. Members of this tribe are known as pochards, or more commonly bay ducks. In North America, there are five common species of bay ducks all of which belong to the single genus *Aythya*: canvasback, redhead, ring-necked duck, and lesser and greater scaup.

The canvasback was not recognized as a species until the early 19th century, presumably because of its similarity to the common pochard of Eurasia, a species with which European immigrants were likely familiar. Alexander Wilson first described the canvasback in his American Ornithology.⁶⁶ He chose the species name "valisineria" after wildcelery, a preferred food of canvasbacks in Chesapeake Bay. Wilson stated that "wherever this plant grows in abundance, the canvas-backs [*sic*] may be expected, either to pay occasional visits, or make it their regular residence during winter . . . while in waters unprovided with this nutritive plant, they are altogether unknown."

The name "canvasback" is believed to have been in use since about 1800¹⁶. The name probably originated in the upper Chesapeake Bay region and is thought to refer to the delicately vermiculated white body plumage of the adult male that resembles canvas fabric³⁴. It is also speculated that the name may have originated from the practice of transporting market hunted birds in canvas bags which were labeled "canvas-back" to indicate their return for reuse. Locally throughout its range, the species has been known by many names including white-back, sheldrake, bullneck, can, canard cheval, gray duck, hickory-quaker, and red-headed bullneck³³.

Geographic Range

The canvasback breeds primarily in the mixed-grass prairie of the central United States, extending from the Dakotas north through the aspen parklands of the central provinces of Manitoba, Alberta, and Saskatchewan. Greatest densities of breeding birds occur in the pothole region of south-central Manitoba, an area that harbors about ten percent of the breeding population.⁶

Although canvasbacks are widely distributed in winter, most birds favor large interior lakes and coastal brackish waters as winter quarters. The greatest numbers of canvasbacks winter in the Atlantic Flyway, especially Chesapeake Bay and coastal North Carolina. San Francisco Bay harbors the largest wintering population on the West coast and recently Catahoula Lake, Louisiana, has been a major concentration area along the Gulf coast (personal communication: D. Woolington). Several detailed breeding and wintering range maps for canvasbacks have been published.^{6,44,50,58}

Canvasbacks use numerous migration routes from the central prairie nesting region to primary wintering areas along the West Coast, the Gulf Coast and Mexico, and the East Coast.⁶ The primary migration route for birds moving to the Atlantic Flyway and down the Mississippi Flyway is southeast from the prairie to staging areas on pools 7, 8, and 9 of the upper Mississippi River near LaCrosse, Wisconsin.⁵⁵ From this location, Atlantic Flyway birds move eastward to major migratory areas such as the Detroit River, Lake St. Clair, and Long Point on Lake Erie. Long-term winter bandings of canvasbacks on Chesapeake Bay by the author show that canvasbacks have about 90% fidelity to this wintering area.

Morphology

The male canvasback is a large, white-bodied duck with a long red neck and head, and a black bib and rump; females are drab with a tan-to-brown head, neck, and bib and gray-brown body plumage. The most distinctive feature of the species is its wedge-shaped head profile formed by its long tapered bill and abrupt crown. The birds form highly visible "white" flocks on large, open, inland and coastal waters during migration and wintering.

Flocks may total over 50,000 birds, although presently few flocks exceed 5000 on the Chesapeake Bay. As an adaptation to diving, canvasbacks have large webbed feet placed well back on their body and must run on the water's surface to attain flight. Canvasbacks are awkward on land and rarely come ashore.

The canvasback is the largest of all pochards world-wide and slightly exceeds the mallard and the American black duck as the largest inland duck in North America. Data collected by the author shows the following average December weights for canvasbacks on Chesapeake Bay: adult males, 1360 g (3 lbs); adult females and juvenile males, about 1280 g (2.8 lbs); and juvenile females, 1175 g (2.6 lb). The heaviest males approach 1700 g (3.75 lbs). During winter, individuals must be examined in-the-hand to distinguish adults and young-of-the-year. Birds can be aged by wing plumage^{12,54} or cloacal characteristics.²³

The canvasback most closely resembles the Eurasian common pochard but differs most noticeably by its superior size (on average it weighs 50% more) and greater whiteness of body plumage. In North America, the canvasback is most similar to and is sometimes confused with the redhead. Close examination, however, reveals many distinct differences, most notably of which are head and bill profile, and bill and eye coloration (see REDHEAD: **Morphology**, this volume). Redheads of both sexes are distinctly darker than canvasbacks, a feature that is particularly useful for identification at great distances. Male canvasbacks have a reddish-chestnut head and neck with a black wash on the face and crown, whereas male redheads have a uniform reddish head and neck with a distinct coppery sheen, a quality quite different from the canvasback. Females of both species are drab, although canvasback females appear more "frosted" with age because of greater vermiculation of feather tips.

Status and Distribution on the Chesapeake Bay

The sole source of canvasback population data for the Chesapeake region is the January winter waterfowl inventory, an aerial census conducted annually since 1955 by the U.S. Fish and Wildlife Service in cooperation with the States. Some earlier data are available on canvasbacks dating back to 1952.⁵⁸

Results of these surveys show a dramatic decline in Chesapeake Bay canvasbacks, both in total numbers and proportion of the continental population wintering on the Bay. Surveys taken during 1952-56 indicate that the Bay harbored an average 267,000 canvasbacks or 53% of the continental population (estimated at 508,000). Later surveys taken over the 25-year period from 1955-1979, show that the Chesapeake Bay averaged 88,650 canvasbacks annually, or 62% of the Atlantic Flyway and 31% of the average continental population (estimated at 285,600).⁴⁷

Surveys over the past six winters (1985-90) show further decline with estimated annual average winter populations of 51,000 canvasbacks on the Bay, amounting to 45% of the estimated Atlantic Flyway population and 19% of the average estimated U.S. winter population of 267,000 birds (unpublished data: USFWS Office of Migratory Bird Management).

Population trends suggest that habitat degradation in Chesapeake Bay, especially the loss of SAV, may be the principal cause for the decline of the Bay's canvasback population relative to the continental population as a whole. The number of canvasbacks on the Bay generally has risen and fallen in proportion to the size of the continental population, except in the period 1970-79 when the continental population increased in response to restrictive hunting regulations and improved breeding ground conditions, while the Bay population remained relatively unchanged.⁴⁷ The relative loss of canvasbacks on the Bay during the 1970's coincides with the dramatic loss of SAV during the same period.

The size of the canvasback population varies most closely with breeding success, which in turn is linked to spring-summer water conditions across the prairies.⁶⁰ Population decline over the past 50 years can be linked to the impact of grain agriculture on canvasback breeding habitats in the prairies. Annual aerial surveys of prairie-breeding waterfowl, known as the Breeding Population Index (BPI), have shown canvasbacks to be the least abundant of the ten common species of prairie ducks. Estimates of numbers of breeding canvasbacks have averaged 556,000 over the past 36 years (1955-90).⁵² The peak count occurred in 1958 (713,000) and the low (385,000) in 1962. Since 1985, drought has resulted in generally poor breeding success for canvasbacks. Populations have increased slowly with closed hunting seasons and gradually wetter conditions. The 1990 Breeding Population Index of 593,000 marked the first time since 1984 that the canvasback BPI exceeded the goal of 560,000 set by the North American Waterfowl Management Plan.¹¹

Analyses of band recoveries have shown an annual survival rate favoring adult males over adult females.^{18,20,37} The most recent analysis of band recovery data found average annual survival rates of 0.56 for adult females and 0.75 for adult males.³⁷ The result has been a sex ratio highly skewed in favor of males.^{1,7} Aerial photography in January 1981 indicated that the sex ratio of nearly 70,000 birds in the Atlantic Flyway was 2.91 males per female.²¹ Higher mortality among females is related primarily to their vulnerability to predators during the breeding period. Canvasback females and young also have been shown to be more vulnerable than adult males to hunting,^{20,41} and it is speculated that they may suffer higher mortality during winter due to a tendency for segregation of the sexes (delayed pairing) and male dominance.^{21,38}

CANVASBACK

Canvasback hunting regulations have been highly restrictive in the region since a season closure in 1972. A three-year (1983-85) experimental season was conducted in five states in the Atlantic Flyway (including Maryland and Virginia). Since 1986 the season has remained closed. During that three-year period, 65% of canvasback hunting permits (20,217) and subsequently 71% of the canvasback harvest (15,852 birds) occurred in the Chesapeake Bay.³⁵ Canvasback hunting seasons currently are based on the three-year average breeding population indices as determined from annual aerial surveys on the prairies.⁶⁵

It is unlikely that this species will reach population levels to permit more than limited hunting in the foreseeable future. Even in good production years, the canvasback is anticipated to provide only a rare trophy for the hunter. Canvasbacks remain not only one of the most popular of waterfowl to sport hunters, but because of their high visibility and accommodation to urban settings (particularly along the Bay's western shore), they enjoy immense popularity and have aroused concern from the non-hunting community as well. The species remains a symbol of Chesapeake Bay waterfowl and is in the forefront of management and research efforts for restoration. The canvasback is a species of special emphasis of the North American Waterfowl Management Plan.¹¹

LIFE HISTORY

Unlike dabbling ducks, which begin pairing in the fall, canvasbacks begin courtship at the onset of spring on the wintering ground. They arrive on the breeding ground paired, and females construct over-water nests most frequently in cattail, bulrush, and whitetop grass. They prefer small, semi-permanent wetlands for nesting, sometimes using larger, more permanent wetlands later in the season. Nesting usually begins in early to mid-May. The typical clutch size is 8-10 eggs. Where the breeding range of the canvasback overlaps with that of the redhead, nest parasitism by redheads commonly detracts from canvasback nest success^{10,61} (see REDHEAD: **Life History**, this volume). The mink is the major nest predator, although the raccoon, a recent arrival to prairie nesting habitats,²⁷ ranks a close second.

Water permanence is crucial to nest success, and declining water levels can lead to nest desertion and catastrophic nest loss to predators.⁶⁴ During periods of drought, canvasbacks may seek better nesting habitats, or forego nesting. Brood survival is variable but is generally higher than in dabbling ducks. Brood survival in canvasbacks has been reported as high as 74% with 5.3 ducklings fledging per successful nest.⁶ Males desert females during incubation and move to large permanent lakes to molt.⁹ Females molt in late summer and become flighted about the same time as young-of-the-year.

Canvasbacks begin migration into the northern Great Plains in September, with major movement occurring in October. Eastern migrants peak in the Great Lakes area in November and arrive on Chesapeake Bay in early to mid-December. Historically canvasbacks arrived on Chesapeake Bay in late October and early November, attracted by abundant stocks of submerged aquatic plants. Special November canvasback surveys conducted by the U.S. Fish and Wildlife Service since 1974 (unpublished data: Office of Migratory Bird Management) indicate that canvasbacks now postpone their arrival, presumably to feed on preferred aquatic plant foods still available in the Great Lakes region.

Banding studies conducted by the author have shown that the highest numbers of young are present on the Bay in December. Aerial photographs have shown a higher proportion of females wintering in North Carolina than in the Bay, verifying that many females and young migrate there, at least in some years.²¹ Canvasbacks winter in coastal brackish waters, but unlike redheads, avoid marine waters or hypersaline lagoons.

ECOLOGICAL ROLE

The canvasback is a seasonal winter resident of Chesapeake Bay. Like other pochards, the canvasback is unable to walk or alight on land, thus its habitats and foods are tied entirely to the aquatic system. Canvasbacks, therefore, depend solely on estuarine bays for their life requirements and are unable to feed on waste grains in agricultural fields, as is now common for dabbling ducks, geese, and swans.

Life history and population statistics suggest that canvasbacks are a species adapted to stable environments.^{26,45} In general, they are long-lived, have a low rate of increase, smaller clutch size, and are suspected to have somewhat delayed reproduction in relation to other prairie nesting ducks. Canvasback yearlings have a lower probability of successful nesting than their dabbling duck counterparts. Canvasbacks are exceptionally traditional and specialized in their use of breeding, migration, and wintering habitats, and this tradition likely is tied to dependable and stable food resources. Their diets are also less variable, usually consisting of a small variety of preferred foods.³⁹ Because of their low reproductive rate, canvasbacks are less able to recover from abrupt losses such as to hunting or disease. Their specialized use of limited habitats makes them less adaptable to changing environmental conditions. Canvasbacks breed most efficiently in low density and are less able to cope with high levels of intraspecific competition as are redheads (see REDHEAD: **Ecological Role**, this volume).

Although canvasbacks share many common aquatic plant and animal foods with other waterfowl, they differ by their

ability to dive and probe bottom sediments with their long, wedge-shaped bills. This gives them unique access to many benthic foods such as tubers and rootstalks, as well as clams and a variety of insects and crustaceans.

Canvasbacks normally feed in water less than four meters deep but are capable of diving to at least twice that depth. Like most ducks, they are essentially herbivorous during the non-breeding period and consume selected plant parts, tubers, rootstalks, winter buds, and seeds, from a wide variety of emergent and submergent vegetation. For example, a 1939 study of 427 birds found that plant foods accounted for 79% of summer and 82% of winter food (by volume).¹⁵ Except during the breeding period, animal foods generally are a small yet variable portion of the diet and become a staple of the diet only when preferred plant foods are unavailable.

Because of their broad distribution and adaptability to a wide range of water chemistries, the true pondweeds are the single most important food resource of canvasbacks throughout their range.³² One species, sago pondweed, is of exceptional value and widely sought because of its abundant seed production in late summer and fall, and its succulent tubers that remain available during winter and spring. Sago pondweed is known to be consumed by breeding adults,^{4,39} juveniles,⁵ molting adults,⁹ and during fall and winter on the prairies,^{3,5,56} in California,⁶⁷ and the Carolinas.^{48,51}

Wild celery is likely the second most important food of canvasbacks but its limited freshwater distribution in the eastern U.S. makes it an important food only in fall and winter. Wild celery formerly grew in great abundance in the upper Chesapeake Bay,^{8,66} but now is much reduced.

Canvasback females and young consume high percentages of animal material to meet the nutritional needs of egg laying and growth, respectively. Aquatic insects (especially odonates, tricoptera and chironomids) and gastropods are consumed in greatest quantities.^{4,5,25,39}

In the upper Chesapeake Bay region, leaves, stems, and rootstalks of wild celery and eelgrass, and seeds of sago pondweed, redhead grass and widgeon grass were the important plant foods consumed in the late 1950's.⁵⁷ Animal foods included the Baltic clam, various other small molluscs, and mud crabs. In a more recent study (1970-79), Baltic clams were found to be the most important food item representing 82% (volume) of the food in 70 gullets and 85% of the food in 323 gizzards examined.⁴⁹ These findings indicate a marked shift in diet resulting from the major loss of SAV in the Bay region.

HABITAT REQUIREMENTS

Structural Habitat

Changes in estuarine habitats that affect canvasbacks relate primarily to the type and availability of food resources. The preferred foods of canvasbacks are rooted submerged aquatic macrophytes which have declined markedly in the 1960's and 1970's,^{17,42,43} coinciding with the decline in the diversity of invertebrate foods consumed by Bay waterfowl.³⁶ These changes do not necessarily place canvasbacks in immediate jeopardy, but they suggest declining habitat quality that ultimately may affect winter distribution and survival, and subsequent breeding performance.

The importance of good food resources for wintering canvasbacks cannot be over-emphasized. In a recent study that examined the relationship between body mass and recapture histories of over 6000 canvasbacks banded in the upper Chesapeake Bay, high early-winter body mass was important in some years to both over-winter and annual survival probabilities.²² Abundant food optimizes over-winter survival probability and provides canvasbacks the best opportunity for timely migration and successful breeding the following spring.

In the 1950's, optimum habitats for canvasbacks in Chesapeake Bay were the fresh and brackish estuarine environments that contained plentiful aquatic plant growth and an abundance of invertebrates.^{57,59} Brackish estuarine waters continue to be the most important wintering habitats because they remain generally ice free at mid-winter and because they harbor the shellfish populations on which canvasbacks now depend.⁴⁹

Recent studies by the author have shown that tidal-freshwater regions, such as the famed Susquehanna Flats, virtually have been abandoned by canvasbacks. A notable exception is the renewed use of the tidal Potomac River following the resurgence of SAV, especially *Hydrilla*.¹³

Water Quality

The degradation of Bay water quality has had the single greatest impact on the foods available to canvasbacks. Excessive nutrients and sedimentation have led to high turbidity that shades SAV and limits its growth.²⁸ Plant vigor has been reduced further by epiphytic growth that is nurtured by high nutrient availability and high water temperature. See SUBMERGED AQUATIC VEGETATION, this volume, for SAV water quality requirements.

Excessive nutrients and turbidity also have led to lowered oxygen tensions in deeper water, widespread benthic anoxia under certain conditions, and sometimes massive mortality among benthic communities.^{40,53} Excessive sedimentation also can smother clam and aquatic grass beds and produce adverse effects on other aquatic life.

SPECIAL PROBLEMS

Disturbance

Although canvasbacks accommodate well to onshore disturbance in urban areas, they do not tolerate activity on the water in their general proximity. Activities such as fishing, clamming, oystering, hunting, and boating are sources of disturbance to wintering canvasbacks. Prolonged or repeated disturbance can prompt permanent movement of birds from traditional resting or feeding areas, as recorded for scaup on the Mississippi River.⁶³ It is clear that canvasback weight, i.e. body condition, can be reduced by prolonged disturbance, particularly if the birds cannot move to other feeding areas. Disturbance can be especially high during warm winters or early springs that permit more commercial and recreational use of the Bay while wintering birds are in residence. Presently, there is limited protection of preferred resting or feeding areas of canvasbacks on the Bay.

Vulnerability of Females to Hunting

Female canvasbacks and young of both sexes are particularly vulnerable to gunning because of their lack of wariness and their general segregation from adult males during fall and winter.^{24,41} Females also are vulnerable to illegal harvest because hunters have trouble distinguishing them from females of other species, especially mallards.

The extent of disproportionate harvesting of females legal or illegal, remains unknown. During much of this period canvasbacks were managed under the area closure concept which prohibited harvesting canvasbacks in traditional migratory or wintering areas but permitted a one bird bag, i.e. a mistake bird, in all other areas. Data now available on the relationship between sex ratio and flock size in the Atlantic Flyway show a disproportionate association of females with small flocks in small water bodies or outlying areas away from large male-dominated flocks.²¹ This evidence indicates that these small, outlying flocks will receive greater exposure to gunning, resulting in a disproportionate harvest of females. Ongoing telemetry studies on Chesapeake Bay by the author will help to answer questions about the magnitude of illegal harvest of females. Presently, canvasback hunting is under complete closure in the Atlantic Flyway, while limited hunting is permitted in Canada and the Pacific Flyway.

Winter Feeding

With increased human populations and urbanization of waterfronts throughout the Chesapeake Bay region, and especially in the upper Bay, feeding cereal grains to wintering canvasbacks has become a widespread activity. Canvasbacks and tundra swans have accommodated to the urban setting and are the primary species affected by this activity. Although the pros and cons of feeding have not been thoroughly evaluated, it is apparent that feeding

has a major influence on the daytime distribution of canvasbacks in this region. Feeding serves somewhat to concentrate birds, associate them with semi-domestic, non-migratory species such as mallards, and foster a dependency on such food. Association of canvasbacks with these more domestic situations may also increase their risk of exposure to disease, predation, and hunting.

Preliminary results of an ongoing telemetry study by the author indicate that juvenile canvasbacks are attracted to and become dependent on such feed.

Oil Spills

A large oil spill in the upper Bay between November and March could be catastrophic to Bay canvasbacks and other waterfowl. Each year millions of gallons of petroleum products, mostly fuel oil and gasoline, are transported and stored near the Bay.

One major threat is posed by rupture of large storage tanks. A spill of this nature in Pittsburgh in 1987 sent 3.5 million gallons of fuel oil hundreds of miles down the Ohio River. A second major threat comes from commercial carriers, mostly barges. The most serious accident in the Bay occurred in February 1976 when a barge loaded with no. 3 bunker oil sank off Smith Point, Virginia, spilling 250,000 gallons. An estimated 30,000 birds, mostly horned grebes and oldsquaws, were lost.⁴⁶ Fortunately large flocks of canvasbacks or other pochards were not in the vicinity of this spill.

Increases in commercial shipping from November through April may increase losses of ducks due to the discharge of generally small quantities of oil from bilge pumpings. Most small spills probably occur at dockside loading facilities. Another source of oil is runoff from storm drains after vehicle accidents or other spills. Canvasbacks also are vulnerable to other potential spills of toxic chemicals or compounds from industrial areas around the Bay.

Contaminants

Numerous pollutants enter the Bay from industrial, urban, and agricultural sources. These pollutants include a wide range of pesticides, agricultural chemicals such as inorganic fertilizers and micronutrients, water soluble fractions of petroleum products from highways and other sources, municipal waste waters which contain metals (chromium, copper, cadmium, lead) and nutrients, and chlorine from drinking water and other sources. Some contaminants can be amplified in the food chain and have direct or indirect effects on canvasbacks.

Reducing pollution in the watershed may be difficult because of the rapid growth of the human population throughout the region. Chronic nonpoint source pollution remains a problem, and domestic and industrial effluents

and agricultural runoff continue to degrade the Bay. Our present knowledge suggests that contaminant levels are within an acceptable range, but we cannot rule out possible sublethal effects to some birds under certain circumstances, or indirect effects such as depletion or contamination of food resources. The direct effects of contaminants may be synergistic, affected by diet (animal versus plant), and they may be exacerbated by winter stress and food deprivation. At the present level of our knowledge, basic dietary changes of canvasbacks on the Bay appears more likely to affect body condition and overwinter survival than the current level of contaminant burdens measured in waterfowl tissues. For more details of the effects of toxic substances on canvasbacks, see EFFECTS OF CONTAMINANTS ON BIRDS (this volume).

Disease

With wintering canvasbacks aggregating in large numbers, an outbreak of disease could have a devastating impact, even wipe out an entire local wintering population. Avian cholera has been the only major recurring disease that has affected wintering diving ducks on the Bay. This disease has occurred in epidemic proportions among oldsquaw and goldeneye, but for unknown reasons has not infected canvasbacks or other pochards.³¹ The greatest disease risk to canvasbacks and waterfowl other than seaducks in the Bay is their association with semi-domestic, non-migratory waterfowl, mostly mallards, that concentrate at feeding stations at urban centers and marinas. Duck viral enteritis has occurred at some of these areas and potentially could affect wild populations. Fortunately, no major disease epidemic has been reported for canvasbacks in the Bay region.

RECOMMENDATIONS

Several recommendations can be made for actions that would improve conditions for canvasbacks on Chesapeake Bay. Management efforts should be designed to improve the abundance and quality of foods available to wintering canvasbacks, which would improve their overwinter survival rates.

Water Quality

Improving water quality would have the most important impact on the aquatic environment of the Bay. Any actions that will improve water clarity, and reduce nutrient burdens and sedimentation are of primary consideration. See BLACK DUCK: **Recommendations** (this volume) for a list of such actions.

Hunter Education

New emphasis should be placed on hunter education and awareness concerning canvasbacks. This effort should be designed to (1) inform hunters of canvasback ecology and

the importance of Chesapeake Bay as a major wintering area for the species, and (2) to improve hunters' ability to identify canvasbacks, especially females. Actions to improve public awareness might include: hunter education courses; highly visible signs at field locations to inform the public of critical canvasback areas; providing information with waterfowl licenses; and distributing information at appropriate outlets such as outfitter stores, wildlife management areas, marinas, boat ramps, and refuges. Efforts to better inform the public should occur at the state, federal, and local level, and should involve waterfowl management, law enforcement, and private conservation organizations.

Refuges

The possibility of establishing refuges for wintering canvasbacks and other diving ducks should be investigated. Areas do exist, (e.g., adjacent to public and institutional lands) that easily could be closed to hunting, boating, or other disturbances. It is particularly important to protect traditional areas for daytime resting. Many urban locations, especially in the upper Chesapeake Bay, also could provide excellent refuge areas.

Research

Research is fundamental to understanding the ecological, nutritional, and energetic relationships of wintering canvasbacks on the Chesapeake Bay. Research is needed to guide our population management and habitat restoration efforts. For instance, we need to understand better how winter nutrition affects overwinter survival and production in canvasbacks. We need to measure the magnitude and identify the causes of female mortality during winter and throughout the annual cycle. Much needs to be learned about habitat use by canvasbacks and the dynamics of their primary food resources.

CONCLUSION

Although canvasback numbers have declined on the Chesapeake Bay over the past three decades, the Bay remains an important wintering habitat for the species, from both a regional and a continental perspective. Habitat degradation, leading to the loss of SAV, has had the greatest impact on Bay waterfowl populations, including canvasbacks. Fortunately, canvasbacks have been able to switch to other available foods, namely small shellfish, for subsistence; otherwise, like redheads, they probably would have abandoned the Bay for more favorable winter quarters.

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REDHEAD

Aythya americana

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The redhead duck historically was one of the most popular game ducks in the Chesapeake Bay region, second only among diving ducks to the larger, more abundant canvasback. An almost exclusive consumer of submerged aquatic vegetation (SAV), the redhead never equaled the prominence of the canvasback as a Bay winter resident, but rather favored more southern winter quarters where plant foods remained available. The redhead was thus an abundant, although sporadic fall and spring migrant, and wintering birds displayed exclusive dependence on SAV.

With similar habitat requirements and life histories, redhead and canvasback populations both have declined with the encroachment of man on breeding, migration, and wintering areas. Both species have been sensitive to ecological changes such as loss and degradation of habitats throughout their range. As

SAV has declined in the Chesapeake Bay, redheads essentially have abandoned the region, while canvasbacks have switched to shellfish as alternate food resources. In the mid 1950's about 70,000 redheads wintered on the bay, representing 40% of the Atlantic Flyway population. They have dwindled over the last decade to 2,000 birds (annual average estimate), representing only 2% of the Flyway total. Among diving ducks, the redhead is the best indicator species of the health of Bay SAV. Clearly, the return of the redhead to Bay waters will mark a major milestone in restoration of the Bay.

INTRODUCTION

The redhead is one of the finest of North American game ducks. It is widely distributed and well known; among the inland diving ducks it ranks second in popularity only to the canvasback. At first glance, redheads and canvasbacks seem somewhat similar in many aspects of their natural history, behavior, and even appearance. Closer inspection, however, reveals many distinct differences in distribution, breeding strategy, feeding ecology, and appearance.

For redheads, the Bay was of high regional importance in the Atlantic Flyway, but far less significant than major winter concentration areas in the Gulf of Mexico. Like the canvasback, the redhead was attracted to Chesapeake Bay by the extensive estuarine habitat and ready availability of SAV, the species' preferred food. One species of submerged vegetation even bears the redhead's name - red-head grass.

The degradation of the Chesapeake Bay, particularly the loss of SAV, over the past several decades has prompted a near-abandonment of Bay waters by redheads leaving only a remnant population today. Restoration of SAV will be necessary before large numbers of redheads will return to the Bay.

BACKGROUND

Taxonomy and Nomenclature

The redhead is one of 14 closely related species of diving ducks world wide called pochards, or more commonly bay ducks.¹⁴ Taxonomically this group belongs to the family Anatidae (waterfowl), subfamily Anatinae (ducks), tribe Aythyini (pochards). In North America, five common species belong in this group and all are members of the single genus *Aythya*.² They are the redhead, canvasback, ring-necked duck, and the greater and lesser scaup.

Like the canvasback, the redhead was not recognized as a species by ornithologists until relatively late, presumably because of its similarity to the common pochard of Europe. Two prominent American ornithologists, John James Audubon and Alexander Wilson, evidently considered them the same species.⁸ Eyton first described the redhead as a separate species in his "Monograph of the Anatidae" in 1838. The first American Ornithologists' Union checklist in 1886 classified the species as *Aythya americana*.

The redhead is known throughout its range by many local names, such as American pochard, red-headed pochard, red-headed duck, red-headed broadbill, red-headed raft duck, fiddle duck, and mule duck.³³

Geographic Range

The redhead breeds throughout the mixed prairie country and adjoining aspen parklands, extending from Nebraska and the Dakotas north to the Minnedosa pothole country (Manitoba) and west to Edmonton, Alberta. Particularly large and dense breeding populations occur at isolated lakes and marshes of the west, especially in the Great Basin. For example, the greatest concentration of breeding redheads in North America occurs in the marshes adjoining the Great Salt Lake, Utah, where the bulk of Utah's 130,000 redheads breed at a density of 355 birds per square mile.⁷

Unlike canvasbacks which rarely winter in salt water, redheads commonly winter in large flocks in marine waters or hypersaline lagoons. Flocks of 100,000 or more sometimes can be seen at the Laguna Madre of coastal Texas and Mexico. This area accounted for 78% of redheads surveyed on the winter inventory from 1948 through 1962, whereas the Chesapeake Bay and coastal sounds of North Carolina accounted for 11.9%, Florida 4.5%, and the west coast of Mexico 2.3%.⁶⁰ Populations of redheads that once wintered in the Chesapeake Bay and North Carolina are believed to have relocated to the Gulf of Mexico. The 1990 winter inventory reported 107,000 redheads on Florida waters, representing 93% of those surveyed in the Atlantic Flyway (file data: USFWS Office of Migratory Bird Management, Laurel, Maryland).

Redheads use several migration routes from breeding grounds to wintering areas. The major Great Plains migration corridor extends from Manitoba to the lower Texas Gulf Coast. Eastward from the central prairie region, migration crosses the Great Lakes to concentration areas at Lake St. Clair, the Lake Erie marshes, and Long Point, Ontario.⁶⁰ From these locations birds either move on to Chesapeake Bay and south along the east coast, or (apparently) fly directly south to the Florida Gulf.⁷

Morphology

Similarities between redhead, canvasback, and common pochard of Eurasia long have been noted by ornithologists. The redhead generally is considered to be closest to the common pochard in overall appearance and biology.^{48,14} Although males of all three species have a reddish-chestnut head and neck, black bib, white belly, and black rump, the redhead is easily distinguished by being darker, having a rounded rather than wedge-shaped head and bill profile, a bluish bill with white and black tip, and a brilliant yellow eye. In North America redheads are sometimes confused with canvasbacks, which have a black bill and a striking red eye. Body and wing plumage of the male redhead is finely vermiculated and dark gray, while that of the canvasback is coarsely vermiculated and white. Thus, at a distance, flocks of redheads look gray rather than white like canvasbacks.

A striking similarity between the adult male redhead and common pochard is their uniformly reddish-chestnut head and neck coloration, whereas that of the canvasback is washed in black. The head and neck plumage of the redhead, however, has a greater degree of coppery sheen and purplish iridescence than either of the other species. The redhead female is quite distinct from the common pochard or canvasback female in being darker and more uniform in color.

Redheads are slightly smaller than canvasbacks, but considerably larger than common pochards. For example, January body mass of adult males averaged 1226 g for New York redheads,⁵² 1326 g for Chesapeake Bay canvasbacks,³⁸ and 849 g for common pochards in the Camargue, France.⁶

In flight, redheads can be distinguished from canvasbacks by their gray appearance, shorter necks, and somewhat more rapid wingbeat, and from scaup by their gray rather than white speculums. Redheads migrate in "v" shaped flocks or long irregular lines, but their local movements are erratic and less organized, resembling scaup rather than canvasback. At great distance, redheads are almost impossible to tell apart from greater scaup, a species they often associate with in brackish or marine waters.

Status and Distribution in the Chesapeake Bay

The Chesapeake Bay redhead population has undergone long-term decline at least since the early 1970's,^{44,46} primarily in response to the catastrophic loss of SAV. Other possible causes for the decline include heavy poaching pressure at an important remote concentration area in Tangier Sound, relatively poor breeding habitat conditions due to long-term drought and unusually cold winter weather in the late 1970's that may have forced redheads to migrate farther south.

Canvasbacks and redheads both have declined with the encroachment of man on breeding, migration, and wintering habitats. Both species have been sensitive to loss and degradation of habitats and other ecological changes throughout their range, especially on prairie breeding grounds. Both are especially vulnerable to hunting and were harvested heavily during the market hunting era. Both species have been managed carefully with highly restricted or complete closure of hunting season during periods of especially low populations, such as 1960-1963 following severe drought in prairie nesting habitats.¹⁶

Reproductive success of both species is tied intricately to prairie breeding habitat conditions, particularly the number and quality of prairie wetlands available for nesting. Although the annual breeding population survey (Breeding Population Index, USFWS Office of Migratory Bird Management, Laurel, Maryland) shows the redhead and the canvasback as the two least abundant species, the survey does not accurately reflect the size of the continental redhead population because it does not cover many major redhead breeding areas.

Redheads generally are more easily censused in winter when they aggregate in large flocks in open water habitats. But their use of wintering habitats is unpredictable, and they often raft as much as several miles offshore where they easily go undetected. The Atlantic Flyway mid-winter inventory between 1980-89 estimated the average annual redhead winter population at 407,500, while over the same period the Gulf Coast survey estimated the average annual population at 758,000. Given the potential for errors, these estimates are generally considered conservative.

The highest Chesapeake Bay redhead populations were recorded during the mid 1950's, a period when all prairie nesting waterfowl populations were high. Winter surveys of 1955 and 1956 found 115,400 and 118,800 redheads on the Bay, with 90% of these birds in the upper Bay of Maryland. During fall and spring migration, redheads used fresh (upper Bay) and slightly brackish (middle Bay) areas where they found an abundance of submerged aquatic plants. During harsh winter periods with icing, the birds moved farther down the Bay to salt estuarine areas where eelgrass and widgeon grass were the primary foods. For example, during monthly aerial surveys in winter 1958-59, Stewart⁵⁵ found all redheads on Susquehanna Flats during November and three-quarters of them there in March. The brackish estuarine bays were the most important areas during the winter, especially Eastern Bay, the Choptank River and the Honga River. In other years large local populations were noted in the Gunpowder-Middle River area,^{55,56} in Eastern Shore tributaries extending from the Pocomoke to Chester Rivers, and in the Patuxent River and middle and lower Potomac areas on the Western Shore.

Drought caused canvasback and redhead populations to plummet in the late 1950's; Bay redheads declined to an annual average of 46,400 during the period 1961-66. Redheads showed further decline in the Bay in the late 1960's, especially following the 1972 storm Hurricane Agnes which devastated SAV.^{23,43}

With the decline of fresh and brackish submerged vegetation in the upper Bay, redheads made a generally higher use of eelgrass and widgeon grass beds in the lower Bay, especially the Tangier Sound area of Virginia. Paralleling this use pattern, numbers of redheads in North Carolina, primarily Pamlico and Core Sound, increased sharply, suggesting a shift in distribution of Bay redheads to these areas. Redheads in North Carolina increased from an annual average of 4,900 in 1970-75 to 40,600 in 1976-82. This eight-fold increase also may have been related to harsher winter weather in the late 1970's, when lengthy periods of cold temperatures and ice cover were common on the Bay.

During the 1980's, numbers of redheads declined to record lows in Chesapeake Bay. Winter surveys reported between 800 and 4,300 Bay redheads with an average of 2,000. North Carolina also experienced a precipitous decline of redheads during the same period, with average estimates of 6,600 birds over the past eight years. The recent decline of redheads in their traditional east coast wintering areas of Chesapeake Bay and North Carolina coincides with the general increase in numbers of birds now wintering along the Florida Gulf coast.

Such abrupt distributional changes seem somewhat characteristic of redheads. For example, ornithologist John C. Phillips noted in his classic 1925 treatise that the redhead "is so particular about its food that it is extremely irregular in its appearance, so much so, in fact, that in regions where it is usually seen in thousands it may almost disappear for a term of years".⁴⁸

LIFE HISTORY

The nesting habitat of the redhead has been summarized as "nonforested country with water areas sufficiently deep to provide permanent and fairly dense emergent vegetation for nesting cover."⁶⁰ These requirements are met in northern prairies of the U.S. and southern Canada, in the aspen parklands of the prairie provinces of Manitoba, Saskatchewan and Alberta, and in the alkaline lakes of the western U.S.

Mixed prairies and parklands form the most extensive breeding habitat for the redhead, but the greatest densities of birds are most often found in the isolated breeding marshes of the west. Here the redhead appears as a colonial nester, an adaptation to these wetlands that seems to belie the origin of the species.⁶⁰ In contrast, the

REDHEAD

canvasback is a species of small water areas where it is isolated; even on large marshes it occurs only in low densities.

The chronology of migration of the redhead from the central plains region is similar to that of the canvasback. Staging occurs in September and major migration is underway in October and November. Most birds are on their wintering grounds by late November.

Redheads leave their more southerly wintering areas in the Gulf of Mexico in late February and at more northerly locations like Chesapeake Bay in mid March. They spend four to six weeks moving from wintering to breeding areas with peak arrival in the central prairie region occurring in April.

The redhead is seasonally monogamous and pairs early on the wintering ground.⁶¹ Early pairing seems to be adaptive to the species' highly developed role as a nest parasite.⁵⁹ Redheads commonly lay eggs in the nests of other waterfowl or other redheads, who subsequently incubate and parent their young. It is typical for such parasitic females to later nest on their own.⁵⁹ Nest parasitism can account for significant production; at the Farmington Bay Waterfowl Management Area, Utah, interspecific nest parasitism accounted for 43% of redhead production.¹⁹

The canvasback is the preferred host of the redhead and where the two species overlap in range, canvasback nests are usually heavily parasitized.^{10,58} Many believe parasitism might detract significantly from canvasback production, whereas it can be beneficial to redhead production. The efficiency of nest parasitism is, however, intricately related to both the density of hosts and parasites, and heavy parasitism can disrupt nesting and result in nest abandonment or poor hatchability.

Redheads typically nest in emergent vegetation commonly of hardstem bulrush or cattail.^{27,29,36,51,62} Nests typically are located in flooded vegetation in close proximity to open water, and wide bands of emergent vegetation in larger potholes usually are preferred over smaller or disrupted stands for nesting.^{27,29}

In the absence of more favorable nesting cover, redheads may nest in nearby upland, usually within a few feet of open water.^{21,34} It is suspected that this practice permits the species early use of newly created wetlands that have yet to develop good emergent nesting cover.

Because of generally widespread nest parasitism, the number of eggs laid by individual redheads is difficult to determine. It is likely that a female would lay 8-10 eggs in her own nest, sometime after laying up to a similar number of eggs parasitically. Some parasitized nests can contain a

large number of eggs; parasitized nests in the Bear River Marshes varied from 19-39 eggs.⁶² A summary of 1380 nests reported from eight different studies found redhead clutch size to range from 8.9-13.8 eggs, with an average of 10.8.⁵⁹

In general, habitat conditions, weather, predation, and breeding bird density (competition) can result in considerable variation in nest success. Redhead nest success has been reported as high as 85% at Gray's Lake in Idaho⁵³ and as low as 15% in Montana where nest parasitism and desertion were instrumental in nest failure.²⁹ A summary of hatching success of 1054 redhead nests from numerous studies, reported an average nest success of 52%.⁷

Inasmuch as redheads normally construct overwater nests, rising water level or wave action can flood or destroy nests,^{30,51} whereas falling water or drought can leave nests exposed to mammalian predators, such as skunks, coyotes, and red foxes. Under normal nesting conditions, mink and raccoons are the most serious threat to redhead nest success, although crows and magpies also can be important. The raccoon recently extended its range into the prairie pothole region in the 1950's and has since become a serious nest predator of prairie ducks.²⁰ In one study in Utah, California gulls destroyed 29% of eggs in poorly concealed redhead nests.⁴⁰

Brood survival is believed to be high, although female redheads are suspected to be less attentive to young than are females of other species. Nearly full-grown broods decline only about 10% from an average size of 6.2 ducklings at hatching.⁷ Because of their late initial nesting, redheads are not known as strong renesters. Only 10% and 15% of redhead nests were determined to be renests in studies in Iowa and Montana respectively.^{29,30} The late nesting of redheads at more northern latitudes, such as in the Canadian prairies, may further reduce opportunity for renesting there. Strong renesting was, however, characteristic of an isolated breeding population of redheads along the St. Lawrence River where parasitism was not a prevalent component of nesting behavior.¹

ECOLOGICAL ROLE

The redhead is a seasonal winter resident of Chesapeake Bay. Because its feet are placed well back on its body, the redhead is unable to walk or land on land and depends totally on the aquatic environment for its life requirements. The redhead, therefore, is unable to adapt to feeding on waste grains in agricultural fields as is now common for dabbling ducks, geese, and swans.

The redhead dives in shallow to medium-depth water, usually 3 m, and where possible, seems to prefer to tip up or dip for food, like dabbling ducks, rather than dive. For example, tipping up is a prevalent feeding behavior

for concentrations of redheads wintering in the Laguna Madre, where the average water depth is about 0.5 m.

In winter, redheads are highly gregarious, commonly congregating in large numbers. Flocking seems an important strategy for synchronizing activity and more efficiently providing food and protection from weather and predators in a large open-water environment.

In comparison to canvasbacks, redheads seem to be more flexible in adapting ecological strategies, as seen in their parasitic nesting habit. The ability to move to more favorable environments at all times of the year seems more evident in the redhead. For example, their transient and sporadic nature on wintering grounds has been noted by several authors,^{25,48,53} and probably relates to their ability to locate the most favorable foraging areas. On the breeding grounds, redheads have shown the ability to pioneer new areas quickly,³⁴ and during the reproductive cycle they have been depicted as more opportunistic foragers, consuming a diversity of available abundant foods rather than a small variety of preferred foods, as noted for canvasbacks.³⁹

The parasitic nature of the redhead and the ability to breed in greater densities than canvasbacks suggests that they have a higher rate of increase and can sustain a higher population given the same amount of habitat. It follows that redheads can both increase their number more quickly than canvasbacks in response to improved environmental conditions, as well as sustain higher populations when faced with high levels of interspecific competition, provided competition comes from species that serve as adequate hosts for nest parasitism.

Food habit studies have clearly shown redheads to be the most highly vegetarian of North American pochards at nearly all seasons of the year. In comparison to the canvasback, two physical characteristics perhaps belie this vegetarian habit: a substantially larger gizzard (personal communication: M.C. Perry, Patuxent Wildlife Research Center) and higher gizzard grit volumes (for grinding fibrous foods).⁴ Redheads prefer rhizomes, seeds, and tubers produced by numerous submerged aquatic plants found throughout their range. The most important plants are those broadly classified in the pondweed family. These include many of the true pondweeds as well as allies including eelgrass and widgeon grass. Members of this group are broadly distributed and tolerate a wide range of water chemistries including fresh, brackish, marine, and alkaline conditions.^{31,32}

Early large-scale food habit studies of redheads found pondweeds to comprise 30-40% of the redhead diet.^{26,12} Other more local studies have also confirmed this finding,^{3,5,9,24,49,50} including studies in the Chesapeake Bay.⁵⁵ Among the pondweeds, sago pondweed is probably most

important to redheads and certainly so to canvasbacks, but several other species are also important. Other submerged aquatic plants important to redheads are the naiads, especially southern naiad and wildcelery. Redheads are also one of few waterfowl that feed heavily on muskgrasses.^{5,12,26,37,39} Other important plants in their diet are the seeds of sedges, especially common three-square and river bulrush, wild rice, water lilies, and smartweeds. Snails and a variety of aquatic insect life are important animal foods.

As shown with other ducks, female redheads increase their protein intake during egg laying by consuming higher percentages of animal foods, such as caddisfly and midge larvae, largemouth bass eggs, and odonate (dragonfly and damselfly) nymphs.^{5,39,63} Breeding redheads have been reported to be more opportunistic foragers than canvasbacks, changing their diet among the reproductive stages, and except during laying, consuming the most abundant foods available.³⁹ Canvasbacks seem to maintain a higher portion of animal food in the diet during the entire reproductive period, whereas redheads revert back to plant foods soon after completion of egg laying. Redhead ducklings also require high protein for rapid growth but seem to eat less animal foods than canvasback ducklings and revert more quickly with age to a plant food diet.^{5,18}

During winter, the redhead also remains a highly vegetative feeder. At the Laguna Madre (Texas), Apalachee Bay (Florida), and Pamlico Sound (North Carolina), rhizomes of shoalgrass have been reported as their primary food.^{11,35,47,57} In the mid-1950's on Chesapeake Bay, redheads fed primarily on the leaves, stems, rootstocks and seeds of various submerged aquatic plants.⁵⁵ In the fresh estuarine bays of the Potomac, Gunpowder and Bush Rivers, several pondweeds including sago and grassleaf pondweed, and naiad were taken in large quantities. Also taken were widgeon grass, waterweed, bulrush, wildrice, and snails. In brackish estuarine bays of the Chester and Choptank Rivers and Eastern Bay, redhead grass and eelgrass were the most important food items. Also taken were corn (as bait), widgeon grass, waterweed, and the marine algae sea-lettuce and hollow green seaweed. Animal foods comprised only 10% of food volume and consisted primarily of mud crabs (Xanthidae) and Baltic clams. In salt estuarine bays, Stewart⁵⁵ found redheads consuming a high percent of bait (corn and sorghum), followed by eelgrass, widgeon grass, and redhead grass.

HABITAT REQUIREMENTS

Expansive shoal-water habitats offering protection from weather and predators and an abundance of food have made Chesapeake Bay an historic migration and wintering region for the redhead. Abundant food increases the chance of survival of migrating and wintering redheads

and affords them the best opportunity for timely spring migration and successful breeding.

The decline of redheads on the Bay coincides with the demise of vascular aquatic plants which has resulted primarily in response to increased turbidity caused by excessive nutrients and sedimentation.²² Redheads can be reestablished in the Bay only through restoration of SAV which in turn depends primarily on improvements in water quality.

Water Quality

Water quality must be improved to allow widely distributed growth of SAV. High nutrient burdens and excessive siltation have led to exceptionally high algal and particulate turbidity that shades SAV and limits growth. Plant vigor has been further reduced by coatings of epiphytes that are nurtured by excessive nutrients and high water temperature. See SUBMERGED AQUATIC VEGETATION, this volume, for SAV water quality requirements. High turbidity has also prompted marked thermal stratification during the summer, which reduces oxygen in deeper water and contributes to expanded benthic anoxia.^{41,53} Such conditions can trigger massive mortality among benthic communities. Guidelines for water quality parameters for five primary redhead food plants are given in Table 1.

SPECIAL PROBLEMS

Illegal Hunting

The majority of the remaining Chesapeake Bay redheads are located in the remote waters in the Smith Island-Tangier Sound area where they are difficult to protect from poaching and illegal sport hunting. An under-cover operation and subsequent raid on Tangier Island by U.S. Fish and Wildlife Service law enforcement agents in the mid 1970's led to over 80 cases and uncovered an estimated illegal kill of 3,000-5,000 redheads over a three-year period. Because of the limited redhead population now remaining on the Bay, these birds must be protected or face even further decline.

Oil Spills

As with all diving ducks using the Chesapeake Bay, a large oil spill during November-April, could devastate populations. Oil is a killer of wintering waterfowl and water birds of all kinds because it destroys the water repellent and insulating quality of the plumage, resulting in death from exposure. In winter, only a small portion of the plumage need be affected to put a bird at serious risk due to heat loss. Even small quantities of oil from bilge pumpings or other sources can be extremely harmful.

The flocking nature of redheads and other pochards means that oil spills could threaten a major portion of the population. A spill in the lower Detroit River in the spring

of 1960 resulted in the loss of over 10,000 diving ducks.¹⁷ The most serious spill in Chesapeake Bay occurred in February 1976 when a oil barge carrying no. 3 bunker oil sank in the lower Bay in Virginia.⁴⁵ As a result, more than 30,000 waterbirds, mostly horned grebes and oldsquaws, were lost. The timing and location of the spill was fortuitous because large flocks of pochards were not present.

Contaminants

Chesapeake Bay receives a substantial burden of toxic chemicals from a variety of sources including industrial, urban, municipal, and agricultural runoff. Many of these chemicals and metals enter the food chain and may be amplified at higher trophic levels. No direct data exists on exposure of redheads to toxics in Chesapeake Bay. However, it is known that SAV can metabolize contaminants from sediments and the water column that may be potentially harmful to redheads. For example, lead and cadmium levels have been found to be higher in Bay SAV than in Bay shellfish.¹⁵ For further information on the effects of contaminants on waterfowl, see EFFECTS OF CONTAMINANTS ON BIRDS (this volume).

Disease

Whenever free-ranging waterfowl aggregate in large concentration, the effect of a disease outbreak could potentially be devastating. Fortunately no major avian epidemics have affected pochards in Chesapeake Bay. Avian cholera has occurred frequently in sea ducks, primarily oldsquaw and common goldeneye in the Bay, but has for unknown reasons not affected pochards²⁸. The greatest threat to redheads is their potential exposure to duck viral enteritis (DVE) that has occurred among local, semi-domestic flocks of mallards and other waterfowl concentrated at feeding stations in urban centers and marinas. Over the last decade, the few redheads that frequent the Bay have been found in remote areas, such as Tangier Sound where there is little risk of exposure to disease generated in urban areas.

Disturbance

Increased commercial and recreational activity on the Bay can increase disturbance to wintering redheads. They show varying degrees of tolerance to on-shore disturbance but are intolerant of boats and low-flying aircraft. During the cold winter months boat traffic usually is restricted to commercial vessels; in exceptionally warm winters however, the Bay attracts increased recreational activity that threatens the habitat for wintering waterfowl.

RECOMMENDATIONS

Water Quality

Improvement in water quality is necessary to restore SAV in the Chesapeake Bay. The actions outlined in the Recommendations section of the Black Duck chapter

would improve water quality and greatly enhance the habitat for redhead ducks on the Bay.

Law Enforcement and Hunter Education

New efforts should be made to inform the public of the plight of the redhead on the Bay and the actions needed to restore this important game duck to Bay waters. It is of special importance that redheads be given the fullest protection under the law and especially in their remaining stronghold in Tangier Sound where flagrant poaching has occurred in the past. Efforts should be made to better inform the public of important redhead wintering and migration areas and to educate hunters to identify this species.

Research

Innovative research should be given full support to guide redhead population and habitat restoration efforts on Chesapeake Bay. Much needs to be learned about nutrient

cycling, contaminants, energetic and nutritional relationships of redheads, and re-establishing SAV in the Bay.

CONCLUSIONS

Redheads formerly used a wide variety of habitats in Chesapeake Bay, as was well documented by Stewart in the 1950's.^{55,56} Under the present degraded water quality conditions, SAV in the Bay has been greatly reduced, making habitat far less attractive for redheads throughout the migratory period, but especially at mid-winter. With restoration of water quality and the return of SAV, the Chesapeake Bay can again be a significant winter habitat for redheads.

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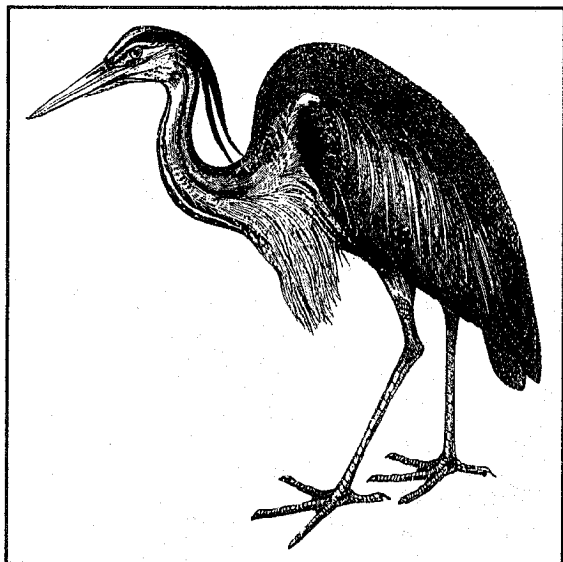
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COLONIAL WADING BIRDS

HERONS AND EGRETS

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Six species of colonially nesting wading birds, the great blue heron, great egret, snowy egret, little blue heron, green-backed heron, and black-crowned night heron, are prominent avian residents of the Chesapeake Bay region. They are top carnivores in a complex food web and, thus may be useful as indicators of change in wetland quality. Except for little blue herons, there is little evidence to suggest that populations in the bay may be declining; in fact, it seems likely that great blue herons are increasing. Although populations may not currently be declining, several factors are of concern: (1) loss of water quality necessary to support submerged aquatic vegetation (SAV) beds (hence good nursery areas for fish and crabs); (2) loss of wetlands due to siltation, agriculture, and sea level rise; (3) disturbance at islands or other colony sites by boaters and other types of human activity. We recommend that water quality conditions be improved so that a large prey base is maintained; that colony sites, especially large ones, receive special status for protection; that riparian

zone buffers be strongly protected; and that feeding areas surrounding colonies receive protection.

INTRODUCTION

Six species of colonially nesting wading birds reside in the Chesapeake Bay region. Most migrate from the region in winter, but small numbers of great blue herons and black-crowned night herons are year-round residents. Overall, numbers of birds have not declined in the past 10-20 years. In fact, numbers of great blue herons may have increased; however, earlier surveys were probably incomplete. The largest nesting colony along the Atlantic Coast is on Nanjemoy Creek, near the Potomac River in Southern Maryland.

The critical factors for sustaining populations of colonial wading birds are: (1) isolated forested islands or extensive bottomland (riparian forests with limited human access and disturbance) for nesting, and (2) extensive wetlands for feeding, with good interspersions of low and high marsh pools and tidal tributaries.

The current Chesapeake problems of high turbidity, low dissolved oxygen, depleted SAV, and increasing Bay water levels all will prove inimical to wading bird populations over time because suitable wetlands require a longer period to develop than they do to degrade.

BACKGROUND

Nomenclature and Taxonomy

Nine species of colonial herons and egrets in the family Ardeidae, order Ciconiiformes, frequently nest together or in close proximity in mixed-species colonies, and feed on a variety of aquatic and terrestrial organisms in the same or similar habitats in the Chesapeake Bay area. Six of these species: the great blue heron (*Ardea herodias*), great egret (*Casmerodius albus*), snowy egret (*Egretta thula*), little blue heron (*Egretta caerulea*), green-backed heron (*Butorides striatus*), and black-crowned night heron (*Nycticorax nycticorax*) will be discussed here in a single

narrative account. Yellow-crowned night herons, and tricolored herons are excluded here because of their small numbers in the Bay. Cattle egrets are not included because they are not truly a wetland species. Except for the black-crowned night heron, all the species discussed here are placed by taxonomists in the tribe Ardeini as being "typical herons". The black-crowned night heron is placed with other night herons in the tribe Nycticoracini.¹

Range

Great blue heron

Great blue herons breed in North America as far north as Nova Scotia on the Atlantic coast, west across southeastern and central Canada to southern and coastal British Columbia, and northwest to southeastern coastal Alaska. From the northern limits of their range they breed south throughout the United States (except in mountainous areas) to Florida and the Gulf of Mexico, and in much of Mexico as far south as Veracruz. One subspecies also nests on the Galapagos Islands.^{1,31} The *occidentalis* group, which breeds in southern coastal Florida, on many islands in the Caribbean, and on the coast of the Yucatan Peninsula and the Los Roques Islands off the northern coast of Venezuela, often was treated in the past as a separate species (the great white heron) but is now generally accepted as being conspecific with the great blue heron.¹ The great blue herons nesting in the Chesapeake Bay area are placed in the nominate subspecies, *A. b. herodias*.²⁷

Great blue herons are year-round residents of Chesapeake Bay. They winter as far north as the southern New England coast, west through southern Ontario, the Ohio River Valley, central Missouri and Nebraska, Wyoming, southern Idaho, and Washington, and northwest along the Pacific coast to British Columbia and southeastern Alaska. From these northern limits they winter throughout the southern U.S., south through Mexico, Central America and the West Indies, to northern South America from Venezuela west to western Ecuador.¹

Great egret

Great egrets are virtually cosmopolitan. They breed in North, Central, and South America in the New World; in Africa south of the Sahara and in Madagascar; in central Europe, Turkey, Iran, and India east through China to Japan; and in most of Southeast Asia, the East Indies, the Philippines, New Guinea, Australia, and New Zealand. In eastern and interior North America they breed from southern Maine south along the Atlantic coast to Florida; west along the Gulf coast to Mexico; inland up the Mississippi River Valley to southern Indiana and the southern Great Lakes in the northeast, and northwest to southeastern Wisconsin and central Minnesota; and also locally in southeastern Saskatchewan and southwestern Manitoba. In western North America they breed from southern Oregon and Idaho south along the coast and inland in

California, Nevada, and southwestern Arizona south into Baja California and along the Pacific coast of Mexico into Central America. Great egrets also breed throughout the Bahamas and the Antilles.^{1,31} The great egrets nesting in the Chesapeake Bay area are placed in the subspecies *C. a. egretta*.²⁷

In North America great egrets winter along the east coast from North Carolina, west along the Gulf coast, through the central parts of Texas, New Mexico, Arizona, and Nevada, to as far north as northern California on the Pacific coast.¹

Snowy egret

Snowy egrets breed only in the New World on the coasts of North America and throughout the Antilles, Central America, and South America as far south as southern Chile and central Argentina. In eastern North America they breed throughout the southern parts of the Gulf coast states and Florida, north along the Atlantic coast as far as Maine, and inland up the Mississippi River Valley as far northeast as southeastern Wisconsin and the southern Great Lakes, and as far northwest as eastern and central Texas, central Oklahoma, and central Kansas. In western North America snowy egrets breed as far north as Northern California, Nevada, southeastern Oregon, southwestern Idaho, Montana, and South Dakota.^{1,29,31} The snowy egrets that nest in the Chesapeake Bay area are placed in the nominate subspecies, *E. t. thula*.²⁷

Snowy egrets winter on the east coast from South Carolina south and west across the Gulf coast; along the west coast from northern California south and east to southwestern Arizona; and throughout the West Indies to Central and South America.¹

Little blue heron

Little blue herons breed only in the New World on the coasts of North America and throughout the Antilles, Central America, and South America as far south as central Peru on the west side of the Andes, and in eastern Peru, central Brazil, and Uruguay on the east side of the Andes. In eastern North America they breed throughout the southern parts of the Gulf coast states and Florida, north along the Atlantic coast as far as Maine, and inland up the Mississippi River Valley as far north as southwestern Kentucky and southeastern Missouri, west through southern Arkansas into central Oklahoma, and south from there through central and eastern Texas. They do not breed on the U.S. Pacific coast, but have bred recently in southeastern New Mexico and southern California.^{1,31} Little blue herons winter as far north as coastal Virginia south and west across the Gulf coast to southern Baja California and southern Sonora, Mexico, south throughout the breeding range.¹

Green-backed heron

There are two recognized subspecies of 'green-backed heron': *Butorides striatus striatus* and *B. s. virescens*, the latter occupying the Chesapeake Bay. The *virescens* group breeds in the New World throughout the eastern and central U.S. south in the West Indies and Central America to Panama where it comes in contact with the more southern *striatus* group. In North America, the *virescens* group breeds as far north in the east as New Brunswick; west across southern Quebec, southern Ontario, northern Michigan, Wisconsin, and central Minnesota; south along the western edge of the Great Plains states (the Dakotas, Nebraska, and Colorado) to north-central New Mexico; west across southern Utah, southern Nevada, and northern California; and north from there to Vancouver Island and southwestern British Columbia.¹ The *virescens* group winters in North America as far north on the Atlantic coast as South Carolina; south and west across northern Florida, south Louisiana, Texas, Arizona, to southeastern California; and as far north on the Pacific coast as western Washington; and south from these northern limits throughout the breeding range to northern Columbia and northern Venezuela.¹

The *striatus* group (considered by some to be a separate species, the striated heron) breeds in the New World from Panama and northern South America in Venezuela and Columbia; south as far as southern Peru, central Argentina, and Uruguay; and in the Old World in Africa south of the Sahara; from the Red Sea to the Gulf of Aden; on islands in the Indian Ocean; east as far north as northern China, in Japan, and throughout southeast Asia, the East Indies, and the Philippines; and south to Australia and southern Polynesia.

Black-crowned night heron

Spendlow and Patton³¹ noted that black-crowned night herons breed on all continents except Australia and Antarctica: "In the Old World they breed from the Netherlands east across central and southern Europe to south-central Russia in the north, and further south throughout India and across China to Japan, the Philippines, and the East Indies; in the Hawaiian Islands south locally through Polynesia; in northwestern Africa south locally through East and South Africa; and in Madagascar. In eastern and central North America they breed as far north as northeastern New Brunswick and Nova Scotia on the Atlantic coast and to the St. Lawrence River inland; west across southern Quebec, southern Ontario, southern Michigan, central Wisconsin, central and northwestern Minnesota, southern Manitoba, central Saskatchewan, and east-central Alberta; and south through the Great Plains to the Gulf coast. In western North America they breed on the Pacific coast as far north as central Washington and southern Idaho inland to the Rocky Mountains. They breed on both coasts and locally inland in Central America south in South America to Tierra del Fuego and the

Falkland Islands. They also breed in the Bahamas and the Great Antilles."¹

The black-crowned night herons that breed in the Chesapeake Bay area are placed in the subspecies *N. n. boactli*.²⁷

In North America, black-crowned night herons winter as far north as southern New England, south and west across the lower Ohio River Valley to southern Texas, central New Mexico, northern Utah, and southern Oregon on the Pacific coast, and from these areas south throughout their breeding range.

LIFE HISTORY

Morphology and Identification

Members of the family Ardeidae typically are long-legged, long-necked birds that hold their necks in an S-shaped position while in flight. They typically catch fish, amphibians, aquatic invertebrates, and sometimes small mammals and birds with their spear-like bills.²⁷ The areas around the eyes and base of the bill are bare and in many species become brightly colored during courtship. The sexes are generally similar in plumage. Several species have plumes, usually on the head, neck, and back, that are used in courtship displays. Descriptions of the breeding plumage of the six species of interest are given below; more detailed descriptions of the nests, eggs, hatchlings, downy young, juveniles, and non-breeding birds are given by Palmer.²⁷

Great blue heron

Adult great blue herons are about 1 m in length, stand about 1.3 m tall, weigh up to about 3 kg, and have a wingspread of up to about 2 m. The forehead and most of the crown are white, the sides of the crown are black down to the eye, and the slender, pointed black occipital plumes grow up to about 20 cm in length. The neck varies in color from a light slate gray to brownish on top; the ventral surface is streaked with black, dark brown, and white. The sides of the lower part of the neck have several long, tapering plumes. The upper parts of the body, sides, and flanks are bluish-gray; the breast and abdomen are black with broad white streaks; and the thighs are chestnut.^{23,27}

Great egret

Adult great egrets are about 80 cm in length, stand about 1 m tall, weigh up to about 1 kg, and have a wingspread of up to about 1.4 m. The entire plumage is white, the bill is yellow, and the legs and feet are black. Great egrets do not have an occipital crest or plumes, but have elongated scapular plumes (aigrettes) that extend beyond the tail.²⁷

Snowy egret

Adult snowy egrets are about 55 cm in length, weigh up to about 375 g, and have a wingspread of up to about 1 m. The entire plumage is white, the bill is black, the lores are yellow, the legs are black, and the feet are yellow. Snowy egrets have elongate plumes on the crown, nape, and lower neck. The scapular plumes extend beyond the tail and are recurved.²⁷

Little blue heron

Adult little blue herons are about 60 cm in length, weigh up to about 400 g, and have a wingspread of up to about 1.1 m. The head and neck are brownish-red, the rest of the body is a dark slate blue. The bill is bluish with a black tip, the lores are a dull greenish, and the legs and feet are bluish-green. There are plumes on the rear of the crown, the lower sides of the neck, and the back.²⁷

Green-backed heron

Adult green-backed herons are about 40 cm in length, weigh up to about 225 g, and have a wingspread of up to about 65 cm. The feathers of the crown are glossy blackish-green and have a bushy appearance when the crest is raised. The sides of the head and all of the neck except for the ventral surface are a reddish-chestnut. The chin, throat, and upper breast are white with blackish stripes. The back and flight feathers of the wings are a glossy grayish-green while the underparts are mostly brownish-gray. The wing coverts have narrow light buff or buffy-rufous edges. The bill is yellowish at the base and brownish-black at the tip, the lores are a yellowish-green, and the legs and feet are yellow or orange yellow.^{23,27}

Black-crowned night heron

Adult black-crowned night herons are about 60 cm in length, weigh up to about 1 kg, and have a wingspread of up to about 1.1 m. They are stockier in appearance than the other five typical herons. The cap is a glossy black, the rest of the head and the 2-3 narrow occipital plumes are white. The back and scapulars are glossy greenish-black; the rump, wings, and undertail coverts are a dark blue-gray; and the underparts are white shading to light gray on the sides. The bill is dark gray, the lores are a paler shade of gray, and the legs and feet are yellowish-orange.²⁷

Nesting Chronology

The annual cycle begins with the arrival of the birds at the breeding colonies in the Chesapeake Bay area in late winter or early spring. Some individuals of some species (e.g., great blue herons, and black-crowned night herons) may remain as year-round residents in this area; in many instances, though, locally breeding individuals leave the Chesapeake Bay area in the fall and are replaced over the winter by individuals from more northern breeding colonies. The ranges of dates presented here come from a publication by Erwin¹¹ that summarized information

from 33 major sources of published and unpublished reports; the data on clutch sizes, incubation periods, and the age at which fledging occurs come from Palmer.²⁷

Great blue heron

In the Chesapeake Bay area, great blue herons may begin breeding activities as early as February. New breeders may continue to arrive at the colonies well into May. The peak of egg-laying occurs from mid-March to mid-June. Clutch size varies from 3-7 with 4 being the mode. The incubation period lasts about 28 days, and the peak of hatching takes place from mid-April to mid-July. Fledging occurs at about 60 days, and most birds depart the breeding colonies from mid-August through December.

Great egret

In the Chesapeake Bay area, great egrets usually begin arriving at the breeding colonies in mid-March and new breeders may continue to arrive into May. The peak of egg-laying occurs from early April to mid-June. Clutch size varies from 3-6 with 4 being the mode. The incubation period lasts about 24-25 days, and the peak of hatching takes place from late April to late June. Fledging occurs at about 6 weeks and most birds depart the breeding colonies from late August through mid-October.

Snowy egret

Snowy egrets usually begin arriving in the Chesapeake Bay area at the breeding colonies in early April. The peak of egg-laying occurs from mid-April to mid-May. Clutch size varies from 3-5 with 4 being the mode. The incubation period lasts about 23 days, and the peak of hatching takes place from mid-May to mid-June. Fledging occurs at about 28 days, and most birds depart the breeding colonies from mid-July through September.

Little blue heron

In the Chesapeake Bay area, little blue herons usually begin arriving at the breeding colonies in early April. The peak of egg-laying occurs from mid-April to mid-May. Clutch size varies from 3-6 with 4 being the mode. The incubation period lasts about 23 days, and the peak of hatching takes place from mid-May to mid-June. Fledging occurs at about 30 days, and most birds depart the breeding colonies from mid-July through mid-October.

Green-backed heron

Green-backed herons usually begin arriving in the Bay at the breeding colonies in mid-March. The peak of egg-laying occurs from mid-April to late June. Clutch size varies from 3-6 with 4 being the mode. The incubation period lasts about 20 days, and the peak of hatching takes place from mid-May to mid-July. Fledging occurs at about 23 days, and most birds depart the breeding colonies from September through mid-October.

Black-crowned night heron

Black-crowned night herons may begin breeding activities as early as February. New breeders may continue to arrive through the end of April. The peak of egg-laying occurs from mid-March to late April. Clutch size varies from 3-5 with 4 being the mode. The incubation period lasts about 25 days, and the peak of hatching takes place from late April to late May. Fledging occurs at about 6 weeks, and most birds depart the breeding colonies from mid-August through October.

Nesting Habitats

The six species of herons under consideration here nest in a variety of habitats throughout their respective breeding ranges (see Spendelow and Patton³¹ for discussions of geographic variation in breeding habitat use by all but the green-backed heron), and the types of nesting habitats used at a particular colony site may be influenced by what other species are present.^{4,6,22,34} Most of the heron colony sites in the Chesapeake Bay area listed in Osborn and Custer²⁶ can be divided into two categories: (1) sites relatively far up the Bay or its major tributaries (either on the mainland or on islands) with sturdy coniferous or hardwood trees more than 7 m tall that were occupied only by great blue herons or mostly by great blue herons and great egrets; and (2) sites on islands closer to the mouth of the bay with shrubby vegetation 2-7 m tall that were occupied mostly by the smaller herons and great egrets. More detailed descriptions of some of these sites were given by Armistead^{2,3} and more information about the nesting habitats used by these six species in the Chesapeake Bay area is given later in this report under **Structural Habitat**.

Distribution, Population Status, and Trends

The number and distribution of breeding colonies of the six species of colonial wading birds in 1988 are summarized in Tables 1 and 2. Discussion of each species follows:

Great blue heron

More than half the estimated population of 11,700 Great Blue Herons breeding in Atlantic coast colonies from Maine to Georgia in the mid 1970's were found in riverine swamps of the Chesapeake Bay region of Maryland and Virginia, and this area contained the five largest Atlantic coast colonies, all with more than 500 breeding birds.³¹ Erwin¹¹ reported 3120 breeding birds in 1975, 4140 breeding birds in 1976, and 3766 breeding birds in 1977, in the Chesapeake Bay area of Maryland. During recent (1988) Maryland inventories [personal communication: D. Brinker, Maryland Department of Natural Resources (MDNR)] more than 7800 birds were found in 34 colonies (Table 1). This may not reflect a population increase as much as an inclusion of more tributary colonies than were inventoried in the 1970's. In the Virginia portion of the

Bay, 1066 breeding birds were reported in 1975, 1100 breeding birds in 1976, 1186 breeding birds in 1977, and about 9060 birds in 1988 in 47 colonies (Table 2). This probably represents both a population increase and an expansion of the survey area. Great blue heron populations in this area had increased in the 10-12 years prior to the 1977 census. Great blue herons are the most abundant wading birds in the mid- and lower Bay area.

Great egret

In 1977 about 11,900 great egrets nested in Atlantic coast colonies from Massachusetts to Georgia; about 2900, or almost one-fourth, of these birds were found in the lower Chesapeake Bay and Delmarva Peninsula regions of Maryland and Virginia.³¹ One of the five largest great egret colonies found in 1977 on the Atlantic coast was at Canoe Neck Creek, Maryland with an estimated 600 breeding birds.¹⁴

Erwin¹¹ reported 670 breeding birds in 1975, 1300 breeding birds in 1976, and 1300 breeding birds in 1977 in the Chesapeake Bay area of Maryland. During recent inventories, about 1100 birds were estimated among 11 Bay colonies in Maryland in 1988 (Table 1). In the Virginia portion of the Bay, 188 birds were reported in 1975, 48 birds in 1976, and 288 breeding birds in 1977.¹⁴ The population had increased at nine colonies in the Bay area of Maryland since the 1960's. In 1988, R. Beck (unpublished data: College of William and Mary) found about 2800 birds at 19 colonies in the Bay (Table 2).

Snowy egret

In 1977 about 26,800 snowy egrets nested in Atlantic coast colonies from Maine to Georgia; about 8350, or just under one-third, of these birds nested in Maryland and Virginia.³¹

Erwin¹¹ reported 1000 breeding birds in 1975 and 1670 breeding birds in 1977 and in the Chesapeake Bay area of Maryland. In 1988, in eight Maryland colonies, 1434 breeding birds were estimated (personal communication: D. Brinker, MDNR; Table 1). In the Virginia portion of the Bay, 640 breeding birds were reported in 1975, 300 breeding birds in 1976, 730 breeding birds in 1977, but only 82 breeding birds were observed at one colony (Fisherman Island) in 1988 (Table 2). Watts Island had snowy egrets in 1988, but they were not counted. Snowy egret populations in the Bay area increased greatly from the 1950's to the 1970's.

Little blue heron

In 1977 about 7400 little blue herons nested in Atlantic coast colonies from Maine to Georgia; but only about 600 of these birds nested in the coastal regions of Maryland and Virginia.³¹

Erwin¹¹ reported a decline from 270 breeding birds at 6 colonies in 1975 to only 90 breeding birds at a single colony in 1977 in the Chesapeake Bay area of Maryland. Brinker (personal communication: MDNR) reported 234 breeding herons at 6 colonies in Maryland in 1988 (Table 1). In the Virginia portion, the 1975 population of 50 birds in 1975 declined to only 12 birds in 1977.¹¹ In 1988, only 78 birds were recorded at Fisherman Island (Table 2).

Green-backed heron

In 1988, only 78 birds were recorded at Fisherman Island (Table 2). Green-backed herons probably were not censused adequately throughout the Atlantic coast during the censuses made for the other heron species in the mid 1970's, and so they were not covered in Spendelow and Patton.³¹ In Maryland and Virginia, respectively, only 56 and 42 breeding birds of this species were reported in 1977, but Erwin and Korschgen¹⁴ noted that only birds found at mixed species heronries were included in these totals.

Erwin¹¹ reported 120 and 26 breeding birds in the Chesapeake Bay areas of Maryland and Virginia, respectively, in 1975. In 1988, in the Maryland portion of the Bay, only 50 birds were reported at 7 locations (personal communication: D. Brinker, MDNR; Table 1). In the Virginia portion, no accurate records were kept of green-backed herons.

Black-crowned night heron

In 1977, about 19,600 black-crowned night herons nested in Atlantic coast colonies from Maine to Georgia; about 5400, or a little more than one-fourth, of these birds nested in the coastal regions of Maryland and Virginia.³¹ The largest Atlantic coast black-crowned night heron colony found in 1977, with about 1650 breeding birds, was located at the mouth of the Chesapeake Bay, at Fisherman Island.¹⁴

Erwin¹¹ reported 700 breeding birds at 7 colonies in 1975, and 1554 breeding birds at 8 colonies in 1977 in the Chesapeake Bay area of Maryland. In 1988, at 7 colonies, about 1962 birds were estimated (personal communication: D. Brinker, MDNR; Table 1), including a newly-discovered location near Baltimore Harbor with 650 birds nesting.¹¹ This is the second-largest night heron colony in Maryland. In the Virginia portion of the Bay, 270 breeding birds were estimated in 1975, 156 birds in 1977, and more than 400 birds in 1988 (Table 2); however, at Watts Island, no counts were made in recent years, so a Bay total is not possible.

ECOLOGICAL ROLE

These species of herons and egrets are top-level predators in the Chesapeake Bay system. They do most of their foraging in a variety of mainly aquatic habitats from the

edges of open water channels, creeks, and mudflats in tidal rivers and marshes, to freshwater ponds and ditches in wet meadows and fields. The species discussed here may use a variety of different feeding behaviors¹⁹ to capture their prey. They feed mostly on small fish, amphibians, crustaceans and aquatic insects.²⁷ All six species of waders are generalists.^{27,36} Based on stomach content analyses (unpublished data: Patuxent Wildlife Research Center), Palmer²⁷ summarized the prey spectrum which, with other data, is summarized in Table 3.

As top-level carnivores, wading birds might be expected to show some evidence of population depression if contaminant levels are high near breeding colonies. Few reliable data are available to assess what pre-industrial population levels were; therefore, the ability to determine population impacts of toxic chemicals on waterbirds is limited.

HABITAT REQUIREMENTS

Water Quality

The six species of heron discussed in this chapter are indirectly affected by water quality, principally as it may limit the availability of prey species. There is a wide variety of suitable prey, each having different requirements for water quality. For many of the non-commercial ("forage") prey, there is relatively little information about water quality requirements. Some environmental data exists on selected prey species (Atlantic silverside, mummichog, striped killifish, white perch, and grass shrimp) and may provide an indication of the relationship between colonial wading birds and water quality. Data on white perch are presented elsewhere in this volume, and data on the other selected prey fish are from Eisler¹⁰ and U.S. Fish and Wildlife Service files. Information on grass shrimp is from Beeston⁵ and B. Welsh (personal communication: University of Connecticut). The essential requirement reported is that these prey species (except for grass shrimp) need 5.0 mgL⁻¹ dissolved oxygen (DO); grass shrimp can tolerate DO down to 1.0 mgL⁻¹. The need for 5.0 mgL⁻¹ is the same level needed by a number of target fish species presented in this report.

In general, water quality needs to be sufficiently high to ensure that extensive stands of SAV and emergent marshes are maintained throughout the tributaries and Bay islands. This is especially critical because sea level rise gradually will reduce the area of wetland available for feeding in many parts of the Bay. In addition, erosion of many islands (e.g., the Poplar group) already is reducing the potential nesting habitat required by wading birds.

Structural Habitat

Aspects of the physical habitat that are required by wading birds are described below:

Colony Sites

The physical habitat required for nesting is somewhat similar for all wading birds. In general, the largest, most persistent colonies are located at isolated sites where ground predator and human access is limited. This does not *always* mean a rural environment, however. Erwin¹⁶ describe a large black-crowned night heron colony in an industrialized area near the Frances Scott Key Bridge near Baltimore. The colony site is, however, isolated by a fence, and trespassing is strictly forbidden. Often colony sites are small islands, but they also may be extensive swamps adjacent to estuarine tributaries.¹⁷ Another prerequisite for nesting is that there be woody vegetation, either shrubs or trees (for great blue herons). The species of vegetation is not critical³¹ since wading birds nest in a variety of shrubs (including myrtle, marsh elder, silverling, etc.) and trees (including both live and dead hardwoods, cedar, several pine species, *yaupon*; etc.) in the Chesapeake Bay area. Rarely, egrets and herons may be found nesting on the ground (with glossy ibises) [personal observation: R.M. Erwin, U.S. Fish and Wildlife Service (USFWS)].

Some species differences in nesting-habitat use exist. Great blue herons are often found in single-species colonies, occasionally with great egrets and others. They nest as frequently in non-island colonies as on islands and are more of an "interior" than coastal species throughout their range. They prefer tall (> 10 m) trees, either live or dead, and use both hardwoods and evergreens in the Chesapeake region. The largest colonies are in woodland swamps adjacent to large tributaries. They avoid areas with human activity. Black-crowned night herons, great and snowy egrets, and little blue herons are more limited than great blues in nesting in mixed-species colonies, usually on islands in the bay region. Great egrets, like great blues, often nest in tall trees, but are frequently found with the intermediate-sized waders in shrubs ranging from 1-4 m in height. Shrubs may be used repeatedly over the years, even when guano has killed the vegetation (personal observation: R.M. Erwin, USFWS). The main requirement seems to be that a nest structure can be built at least 1 m above the ground, presumably to reduce the risk of mammalian predation.

Green-backed herons are often considered semi-colonial because they frequently nest solitarily as well as with other herons and egrets.²⁷ In addition to nesting in shrubs and small trees, they are often found nesting (1-8 nests) on duck blinds throughout the Bay area. For this reason, it is very difficult to estimate the total population of this species.

Feeding Habitats

Although colony sites are well-documented in the Chesapeake Bay, much less is known about other habitat requirements, such as feeding, roosting, and migration

stopover sites. Feeding habitats are quite diverse for wading birds in the Bay area. These include both tidal and non-tidal rivers and creeks, brackish and fresh marshes, ponds, lakes, and impoundments, and even aquaculture facilities (personal communication: L. Terry, U.S. Department of Agriculture).

Almost no research has been conducted on Chesapeake Bay wading birds to assess their feeding habitat use. However, Erwin *et al.*¹⁶ monitored black-crowned night herons flying from a colony to landing sites. Of 44 herons followed, most landed within 5 km of the colony, in industrialized parts of the Baltimore-lower Patapsco River estuary. In another estuarine setting in North Carolina, Custer and Osborn⁸ used aircraft to follow individual birds of nine species over one season (May to mid-July). They found that great egrets were the only wading birds to use SAV (*Zostera*) beds extensively, and this use was restricted to low tide. Great and snowy egrets generally used feeding areas near (< 4 km) the colony, but some fed up to 28 km away. A 6 km radius included 75-80% of all flights of snowy (n=38) and great (n=145) egrets. Over 80% of all herons followed landed in saline (saltmarsh) habitats; only 7% flew to fresh water. A 10 km radius is our best estimate of the extent of wetland habitats adjacent to colonies as a feeding habitat requirement. We recognize that this area is probably too small, especially for great blue herons. Recent (1987-88) colony sites and their associated wetland habitats are identified in the Map Appendix. Because wetlands along the Atlantic Coast have declined significantly in recent years, emphasis needs to be placed on preserving these areas.

Other Habitats

Other than colony site locations, and indirect association of feeding habitats, we know little about "other" habitat requirements such as migration stopover sites, or fall/winter roosts. All wading bird species, except great blue herons and night herons, migrate from the bay region in September and October.¹¹ Fall or winter roosts of the two herons include Conowingo on the Susquehanna River (100-150 great blues, 20-30 night herons), the Westport area of Baltimore (20-30 night herons), Stony Creek in northern Anne Arundel County (night herons), and a fall roost at Deal Island Wildlife Management Area, Somerset County (personal communication: R. Ringler, Maryland Ornithological Society). Probably all the wildlife management areas and wildlife refuges on the eastern shore of Maryland are important stopover areas for wading birds migrating south, but few data exist except in the form of monthly wildlife use reports filed by refuge personnel. A winter bird atlas has been initiated in Maryland (personal communication: D. Bystrak, S. Droege, C. Robbins, USFWS) but this program is not designed for waterbirds.

SPECIAL PROBLEMS

Disturbance

Avoidance of disturbance, both by natural ground predators and humans, probably explains the predominant use of island or inaccessible mainland sites by most species of colonial wading birds. However, as the population adjacent to the Bay continues to grow, more and more colonies, roosts and feeding areas will be subject to boating and pedestrian disturbance. Land managers need guidance to establish safe buffer distances around nesting colonies. Habitat Suitability Index models have been published which suggest safe distances of 150 m (over water) and 250 m (over land)³⁰ for great blue herons, and 1000 m for great egrets.⁷ These were only crude estimates, however, and were not based on empirical data. Erwin¹³ published guidelines for wading birds based on field tests in numerous colonies in coastal Virginia and North Carolina. During nesting, wading birds flushed at approach distance of 12-93 m (mean 53 m); however, it was cautioned that these tests were conducted during late incubation periods when birds are more tenacious than earlier in the season. A conservative distance of 200 m was recommended early in the season for protective sign-posting at colonies.

Disturbance at feeding sites is probably less crucial because, in areas with human activity, birds readily habituate to people, especially people in vehicles. Waders feeding in impoundments can be approached within 5 m by automobiles along wildlife refuge drives (personal observation: R.M. Erwin, USFWS).

Contaminants

Numerous concerns have been raised over the levels of pesticides, herbicides, and industrial pollutants and their potential impacts on the Bay's organisms. Unfortunately, few studies have been directed at the effects of contaminants on the breeding biology of colonial wading birds in the Bay area. Ohlendorf *et al.*²⁴ conducted an extensive survey of wading bird eggs throughout the East Coast region. The only collection of wading bird eggs from Chesapeake Bay was at one location in St. Mary's County on the Potomac River where two green-backed heron eggs were collected. Samples had low residue levels of both DDE (mean 0.51 mg kg⁻¹) and PCB (1.6 mg kg⁻¹), which were below levels known to induce some reproductive impairment. Concentrations of > 3 mg kg⁻¹ for DDE (wet weight) are considered potentially harmful for black-crowned night herons,⁹ as are concentrations exceeding about 10 mg kg⁻¹ PCB.^{28, 33}

Ohlendorf *et al.*²⁵ conducted a survey of residues in wading birds found dead, several of which were from the Bay region. Compared to birds from the Great Lakes, Chesapeake birds had lower levels of most contaminants. No great blue or green-backed herons, or any snowy

egrets, from the main part of the Bay appeared to have died from organochlorine poisoning.

See EFFECTS OF CONTAMINANTS ON BIRDS, this volume, for more information.

Eutrophication

Eutrophication, in itself, is indirectly related to wading bird populations through feeding habitat quality in the Bay. If eutrophic conditions do not improve to the level where SAV beds become reestablished throughout the watershed, the quality and quantity of foraging habitat will remain limited.

All six species of egrets and herons are extremely omnivorous.^{27, 36} They feed in a variety of habitats including open water channels, mudflats, tidal and freshwater marshes, and even wet meadows and fields. Prey taken depend on time of year, geographic location, and micro-habitat use. Based on stomach analyses, Palmer²⁷ summarized the prey spectrum.

Even in estuaries with poor water quality, i.e., turbidity, hypoxia, etc., sufficient numbers of tolerant prey species such as killifish, grass shrimp, and blue crabs exist to support nesting populations in a number of urban areas. Nonetheless, this probably represents a depauperate bird fauna, since better water quality would enhance wetland quality, in turn producing more prey to support a larger avian biomass. Water quality standards should be sufficiently high to support dense stands of SAV and emergent plants.

RECOMMENDATIONS

Several specific recommendations for improving habitat quantity and quality in the Chesapeake Bay for wading birds are listed:

Water quality

In spite of the indication that toxics are not a problem for wading birds, the general high turbidity, low-oxygen conditions are not conducive to high fish and invertebrate densities in wetlands. Several species (e.g., grass shrimp and mummichogs) survive poor water-quality conditions, but with improvement of conditions, more large-bodied fishes such as bass and perch would be available as prey biomass. Stringent efforts are necessary to reduce storm-water run-off, agricultural drainage, and boat discharges. Nutrient input from non-point sources needs special attention.

Nest-colony protection

Some type of special designation should be given traditional, large colonies to protect *both* the colony site, with a surrounding buffer of 200 m, and the wetland-foraging

area around the colony site. Wetlands within 10 km of major colonies should be granted special attention.

Island protection

Excessive erosion can be reduced by a variety of methods including both structural and non-structural means. Stabilization using *Spartina* plugs could be used in some areas, adding dredged material to offset losses, or building islands with both dredged materials, derelict vessels (barges), or other structures are methods that have had success in other areas. In general, building seawalls and bulkheading are both expensive and ineffective in many cases.

Riparian zone protection

Silvicultural practices, sand-mining, and other agricultural activities impact forest-nesting herons and egrets. Protection of these areas at critical times of year (February-July for great blue herons) would be advised. Also, buffer distances of at least 250 m from the edge of the colony would help mitigate disruption.

Research

Additional research is needed to determine the foraging ranges of wading birds and their temporal patterns of habitat use, i.e., do they forage in different places at different times of the season? Much more information is required on how migrant wading birds use wetlands, and where wintering birds feed. We also have little information about existing roost sites. We need to know how traditional these are over time and what the land protection status is of major roost areas.

Biomonitoring

Wading bird colonies can serve as a valuable indicator of environmental quality. Colonies need to be monitored annually in Chesapeake Bay, and all coastal habitats. The changes in key parameters such as chick growth rates, chick tissue contaminant levels and population sizes can then be used to evaluate environmental changes in the Chesapeake and other coastal region.

CONCLUSIONS

The numbers of wading birds in the Chesapeake Bay region probably have remained stable or increased over the past 15-20 years. However, the recent inventories in Maryland, 1985-88 were more thorough than those con-

ducted in 1976-77, thus direct comparisons are invalid. It seems certain that black-crowned night herons have increased in both the Maryland and Virginia portions of the Bay. In 1988, the second largest night heron colony in the State of Maryland was located in the Baltimore Harbor area, near the Frances Scott Key Bridge in Dundalk, Maryland. This colony grew from only about 25 nests in 1979 (personal communication: R. Ringler, Maryland Ornithological Society) to about 320 in 1988.^{15,16} The largest great blue heron colony (Nanjemoy Creek along the Potomac River) in the northeastern United States, continues to grow, from 700-800 nests in the late 1970's to 1200-1500 nests in recent years¹⁷ (personal communication: D. Brinker, MDNR).

One trend of concern, however, is that the number of colony sites appears to be decreasing, at least in Maryland.¹⁸ Thus, some colonies may be increasing, but at the expense of a number of small colonies. Sea-level rise and island erosion in the Bay may be responsible in part for the loss of waterbird colonies. Erosion is rather dramatic in the Poplar Islands group, in Eastern Bay, at the South Point Islands, and at Smith and Tangier Islands in mid-Bay. With fewer nesting site options, wading birds become more susceptible to predation, disease, and natural disasters (e.g., oil spills).

Of equal or greater concern, with sea-level rise and development pressure, is the loss of wetlands required for feeding sites during nesting and migration periods. Fortunately, several of the wading birds do not require extensive, high quality marshes for feeding. Black-crowned night herons, great blue herons, and green-backed herons all feed in fairly polluted urban-suburban environments; toxic chemicals do not appear to be a limiting factor in the Bay region for these species of wading birds. However, the tolerance shown by a few species should not necessarily be assumed to pertain to all. Further, even though some species show a tolerance of poor water quality in estuaries, the population sizes of all wading birds would certainly be enhanced with higher-quality wetlands with a larger prey biomass.

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COLONIAL WADING BIRDS

Table 1. Estimated numbers of breeding wading birds on the Maryland portion of Chesapeake Bay during 1988.¹⁸ Estimated number of breeding wading birds calculated from known breeding pairs.

GREAT BLUE HERON		GREEN-BACKED HERON	
Nanjemoy Creek	>2400	Dickinson Island	18
Canoe Creek Neck	1238	Opossum Island	16
Coaches Is.	1080	Jean's Gut	6
Barren Is.	720	St. Pierre's Island	4
Black Swamp Creek	392	Rhodes Point South	2
Cherry Island	354	Easter Point	2
Romney Creek	340	Chaisey Point	2
Fin Creek	242		
Federalsburg	172	LITTLE BLUE HERON	
Elk Neck SF	160	Point Comfort	146
Mattawoman Creek	160	Pines Hammock	64
Cox Creek	102	Rhodes Point South	10
Piney Is. Point	92	Rhodes Point Road	6
Moss Pond	40	Ireland Hammock	6
Bolingbroke Is.	40	Poplar Island	2
L. Queenstown Creek	36		
Worsell Manor Rd.	32	SNOWY EGRET	
Hazard Point	30	Point Comfort	998
Adam Island	28	Poplar Island	304
Bloodsworth Pt.	26	Rhodes Point South	52
Thomas Is. Gut	22	Pines Hammock	32
Dyer Creek	20	Hog Neck	32
Zekiah Creek	18	Cherry Island	8
Opossum Is.	16	Easter Point	6
Hog Neck	14	Chaisey Point	2
Race Hog Neck	12		
Baybrush Pt.	10	BLACK-CROWNED NIGHT HERON	
Kirwan Creek	10	Point Comfort	1242
Bishop's Head Pt.	10	Key Bridge Toll	648
Clark's Wharf	10	Cherry Island	44
Sillet Point	8	Rhodes Point South	10
Holland Is.	8	Chaisey Point	10
Raccoon Creek	6	Rhodes Point Road	6
Coursey Point	2	Ireland Hammock	2
GREAT EGRET			
Barren Island	324		
Cherry Island	238		
Poplar Island	114		
Pines Hammock	86		
Ireland Hammock	80		
Canoe Creek Neck	80		
Point Comfort	48		
Race Hog Neck	38		
Rhodes Point Road	34		
Hog Neck	24		
Holland Island	16		

Table 2. Estimated numbers of breeding wading birds on the Virginia portion of Chesapeake Bay during 1988. Estimated numbers of breeding wading birds calculated from known breeding pairs. N/A=Colony active in 1987 or 1989, but not in 1988. (unpublished data: R. Beck, College of William and Mary).

GREAT BLUE HERON		GREAT EGRET	
Shacklefords I	1068	Fisherman's Island	604
Roxbury I	942	Hampton egrets	482
Yorktown	940	Little Creek	474
Indian Head	808	Lancaster II	466
Pleasant Ridge II	644	Norfolk South	242
New Pt. Comfort	542	Tangier Island	116
Passapatancy	474	Norfolk N.	110
Hog Island I	404	Roxbury I	74
Tangier Island	354	Pleasant Ridge II	54
Richmond	226	Knotts Island	54
Knotts Island	220	Yorktown	30
Watts Island	218	Courtland	24
Ware Neck I	182	Hog Island I	22
Toano	178	Dendron I	16
Gloucester I	156	Tunstall II	14
Tunstall I	142	Seven Pines I	8
Seven Pines I	140	Tunstall III	8
Dendron II	136	Pleasant Ridge I	6
Clay Bank II	118	Watts Island	Present (no count)
Courtland	110	Kempsville	N/A
Hylas	96	Seven Pines II	N/A
Hog Island II	86	Dendron II	N/A
Montross II	82	Little Creek	N/A
Norge	78		
Charles City	64	GREEN-BACKED HERON	
Tunstall II	64	Fisherman Island	78
Quinton '88	60		
Surry II	58	LITTLE BLUE HERON	
Dendron I	56	Fisherman Island	78
Lively	42	Watts Island	Present (no count)
Clay Bank I	36		
Yellow Tavern I	36	SNOWY EGRET	
Morattico	34	Fisherman Island	82
Seven Pines II	34	Watts Island	Present (no count)
Walkers	30		
Shacklefords II	26	BLACK-CROWNED NIGHT HERON	
Surry I	26	Fisherman Island	434
Tunstall III	24	Watts Island	Present (no count)
Beaulahville	22		
Loretto	20		
Pleasant Ridge I	18		
Moyock	18		
Gloucester II	12		
Brandon II	12		
Brandon I	12		
Roxbury II	6		
Montross I	6		
Yellow Tavern II	N/A		
Midlothian	N/A		
Providence Forge	N/A		
Chesterfield	N/A		
Elliotts Creek	N/A		
Providence Forge	N/A		
Quinton '89	N/A		
Ware Neck II	N/A		
Tunstall IV	N/A		

COLONIAL WADING BIRDS

Table 3. Prey taken by colonial wading bird species in different U.S. localities. n = number of stomach samples, asterisks indicate significant amounts.

Species	Fishes	Crustacea; large invertebrates	Aquatic insects	Herptiles	Small mammals	Miscellaneous	Reference
Great Blue Heron (n=189)	72%	9%	8%	4%	5%	2%	Palmer ²⁷
Great Egret	Dominant	Common			few		Erwin ¹² , Palmer ²⁷ Willard ³⁶
Snowy Egret	> 50% *	34% *			*		Willard ³⁶ Palmer ²⁷
Little Blue Heron (n=46)	27%	45%	17%	*	*	*	Palmer ²⁷
Green-backed Heron (n=255)	45%	21%	24%			10%	Palmer ²⁷
Black-crowned Night Heron (n=117)	52%	22%	16%	6%	3%		Palmer ²⁷

OSPREY

Pandion haliaetus

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Ospreys feed almost exclusively on live fish. Their position as a consumer at the top of an aquatic food-chain proved hazardous from the 1950's through the early 1970's when organochlorine pesticides (DDT) adversely affected their reproductive success leading to a population decline. The banning of some persistent pesticides during the 1970's enabled Chesapeake Bay osprey populations to increase to an estimated 2,000 pairs by the 1980's. Pesticides are still used in South American wintering areas, however, the effects on Chesapeake Bay osprey populations is unknown.

Osprey foraging efficiency and energy budgets and the prey type, abundance, and nutritional value are poorly understood and need research. This is especially important in view of reported deteriorating water quality and decreasing fish populations. Management of ospreys in the bay should include enhanced public awareness of osprey ecology, creation and maintenance of artificial nest structures, monitoring of foraging and nesting success, and analysis of eggs and body tissue for presence and effects of toxic chemicals and metals.

INTRODUCTION

Ospreys are the only North American hawk that feeds almost exclusively on live fish. The large waterfront nest, the spectacular aerial plunge into Bay waters for fish, and the recovery from a serious population decline has endeared the osprey to observers of Chesapeake Bay. Ospreys are known for their tolerance of non-threatening human activity and their adaptability to artificial nest structures in close association with waterfront residences.

In the 1950's through the early 1970's tissue accumulation of organochlorine pesticides reduced osprey reproductive success, leading to a serious population decline. Banning of some persistent pesticides during the 1970's has enabled osprey reproductive success to rebound. The population grew during the 1980's, and now approaches 2,000 breeding pairs, representing 20% of all ospreys nesting in the contiguous United States.

The osprey's high visibility, ease of study, and its position at the top of the aquatic food chain make it a valuable indicator species for detecting habitat destruction, dwindling fish populations, and environmental contamination in Chesapeake Bay.

BACKGROUND

The osprey or "fish hawk" belongs to the order Falconiformes, family Accipitridae, and subfamily Pandioninae. The osprey's geographic range includes shallow water estuarine, river, and lake habitats of all continents except Antarctica. Most osprey winter in the tropics and nest in temperate to sub-arctic latitudes.³²

Ospreys three years old or older usually mate for life, and return each subsequent year of life to nest in their Chesapeake natal area during March-August. Ospreys nesting further north use Chesapeake Bay resources during migration periods in April-May and September-October. Ospreys are distributed throughout the tidal Chesapeake

Bay, its tributaries, adjoining waterways, and adjacent impounded waters. Nesting is common along wide, shallow portions of tributaries, but uncommon along narrower headwaters, streams and small impoundments. Nesting may not occur in some highly populated or polluted areas such as the Patapsco and lower York Rivers.

Intensive investigations into the reproductive success of ospreys first began in the early 1960's. Interpreting results of these early studies was difficult because the reproductive rate of a stable osprey population was not known. Consequently, conclusions were based on comparisons among regions.^{1,3,34,37}

A statistical model based on band recoveries for New York and New Jersey ospreys from 1926-61 was subsequently used to determine mortality rates, and to calculate that each breeding age female must produce 0.95 to 1.30 young annually to ensure population stability. The statistical model includes assumptions concerning breeding age, sex ratios, mortality rates, and band reporting; also it excludes inaccessible nests and any nest without eggs. The effects of artificial nest sites, immigration, pesticide residues in tissues, and human disturbance could conceal a trend in population status. The model remained the accepted method for determining population status through the 1970's despite its shortcomings.^{13,43}

Studies in 1966-71 in Eastern Bay, central Choptank River, lower Potomac River, and all the Virginia tributaries found osprey productivity below the range estimated necessary for population stability, while Smith Island and some Choptank River tributaries produced within the stability range. Poor reproductive success in these studies was attributed to egg failure. The Chesapeake population was estimated to be declining 2-6% annually. Presence of DDE, a metabolite of DDT, in osprey eggs has been correlated with eggshell thinning. DDT metabolites have been found in all Chesapeake osprey eggs analyzed. Chesapeake osprey eggshell thinning during the 1960-1970's ranged from 6-24% and was primarily responsible for large numbers of addled, cracked, and broken eggs. DDT has been banned in the U.S. since 1972.^{14,19,40,41,42,43,44,45,51,52,61,62,63,64,67}

Productivity data after 1971 are available only for the Eastern Bay and Choptank River areas where production increased appreciably in 1972 and remained within or above the stability range through 1979. No Chesapeake population productivity data are available for the 1980's.^{42,43,44}

LIFE HISTORY

Arrival - Courtship - Nest Building

The most intense period of courtship and nest building by Chesapeake ospreys is mid-March through mid-April. Ex-

perienced breeders begin arriving at previously used nest sites in late February-early March with males preceding females by a few days. Courtship and nest building or nest repair may begin when the pair is reunited. Less experienced birds arrive or initiate courtship a little later, whereas first-time nesters may spend several weeks locating a mate and nest site. Both birds of a pair collect corn stalks, branches, and shoreline debris which they arrange into a bulky nest, about a meter in diameter and sometimes as high, on a dead snag over or near water, or on the pinnacle of a man-made structure (utility pole, nest platform, duck blind, or marine navigation aid).

Eggs

Egg laying and incubation takes place mostly between mid-April and late May, and clutches may be replaced if lost prior to mid-May. The normal clutch of three beige, chicken-size eggs with blotches of chestnut, olive, and browns are incubated principally by the female for 38-42 days after the laying of the first egg.

Young

The period of late May through June is the most intense for activity of the young. Nestlings are brooded by the female, fed fish, and begin to resemble adults by 40 days of age when they commence daily strenuous exercise in preparation for flight at about 55 days of age. Family units remain intact near the nest site through July while fledglings acquire fishing skills.^{53,55}

Migration

Adults begin fall migration as soon as fledglings become independent. Chesapeake juveniles migrate the last week of August along a narrow Atlantic coastal path. They leave the U.S. by September, continue south through the Greater Antilles, and arrive at the Colombia wintering grounds by mid-October. Ospreys winter (December-February) primarily on the large islands of the Greater Antilles (Cuba, Hispaniola, Puerto Rico), Lake Maracaibo and the Orinoco River in Venezuela, the Cauca and Magdalena River systems in Columbia, and the multitude of tributaries making up the Brazilian Amazon. Juveniles remain south of the U.S. at least 16 consecutive months; only 25-54% of the two-year-old age class return to their natal area, but these birds do not actively nest. Band recoveries of breeding age ospreys, three years or older, occur at a mean latitude of 32°N (Savannah, Georgia) in March, indicating equivalent migration distances are traveled 2-3 times faster during the spring than fall.^{15,18,33}

ECOLOGICAL ROLE

The osprey's diet consists almost entirely of medium-sized fish which are captured just beneath the surface by plunging feet-first from flight into the water, then rising into the air by wing action high over the back. They are especially attracted to surface schooling and spawning fish, but are

basically opportunists, feeding on any species that is plentiful or readily accessible in any body of water at any given time. Finding and capturing fish is an arduous task, and many variables can influence the outcome, such as the season, geographical location, atmospheric conditions; the bird's age, weight, and fishing ability; and the fish species, size, nutritional value, abundance, and ecology. Water quality is another important variable influencing the osprey's presence and foraging success. Eutrophication, depletion of benthic fauna, and toxic contamination may cloud water and suppress fish populations, while suspended materials, turbidity, and surface rippling obscure visibility for fishing ospreys. Fish can be sources of organochlorine compounds and toxic elements that can cause osprey reproductive failure when accumulated in toxic concentrations, and they also may be vectors for internal parasites or diseases of ospreys.

Predation

Raccoons are an important predator, having been implicated in 2% of the lost eggs and some young from shoreline and terrestrial Chesapeake nests. Predation by raccoons is more serious in developed areas where human garbage sustains a large raccoon population, but installation of predator guards can preclude this predation. Norway rats and American and fish crows have been observed robbing eggs from unattended nests. Great blue herons, bald eagles, and great horned owls have been reported preying on osprey nestlings; horned owls and golden eagles have killed adult ospreys. The exposed nesting habits of ospreys make them vulnerable to the much larger and agile eagles and to nocturnal predation by the more powerful great horned owl.^{1,21,25,28,32,37,40,43,63}

Interspecific competition

Interspecific competition can influence the success and local distribution of nesting ospreys. The safety and remote location of offshore structures in the Chesapeake Bay attract several species of nesting birds. Nesting snowy egrets, green-backed herons, Canada geese, American black ducks, mallards, barn owls, barn swallows, common grackles, and European house sparrows share sites with ospreys, and sometimes several species nest simultaneously on the same hunting blind within inches of other species in relationships that are not always friendly or conducive to successful nesting. Ospreys may stoop (attack while diving) on nesting snowy egrets, green-backed herons, Canada geese, American black ducks, mallards and barn owls that flush from the same nest site upon the osprey's approach; ospreys have been known to kill herons and owls. They may also stoop on great blue herons, turkey vultures, bald eagles, red-tailed hawks, herring gulls, and great black-backed gulls straying near active osprey nests.

Conversely, great blue herons, Canada geese, bald eagles, red-tailed hawks, herring gulls, great black-backed gulls,

common terns, least terns, eastern kingbirds, and red-winged blackbirds sometimes attack ospreys. Bald eagle territorial behavior lowered reproductive success and forced relocation of nearby nesting ospreys in a Florida study. Canada geese have been observed trying to force ospreys from their nest, while mallards have parasitized, replaced or forced relocation of actively nesting ospreys. Intraspecific competition may be important in areas where nest sites are dense, but there is currently no documented evidence supporting this hypothesis.^{1,5,6,22,25,27,43}

HABITAT REQUIREMENTS

Food Requirements

Ospreys require an ample supply of medium-size fish to thrive. Males brought 2.5-8.3 fish per day to mates with varying nest contents; non-tidal lake nests with nestlings received fewer fish than comparable tidal Bay nests (Table 1). Preincubation fish deliveries (3.6) are about the same as deliveries during incubation. The size and weight of prey species from several studies (Table 2) indicate that ospreys commonly capture abundant species approximately 15-25 cm long, weighing 75-200 g. A range of 0.7-1.2 kcal g⁻¹ of flesh is given for 12 species of fish caught by ospreys. The size, age, sex, physical condition, and percent of fish indigestible cause the nutritional value of fish to differ between and within species. For example, a gravid spot would be nutritionally richer with its fat than a non-spawning spot, whereas proportionally more of the spot would be eaten than of a bony-headed toadfish. The daily catch rate, average fish weight, and average kcal g⁻¹ of flesh were used to estimate that a nesting male feeding a mate and three young brought 1125 kcal of fish to the nest daily.^{23,32}

Energy budgets may be slightly different for each individual osprey; however, current estimates for daily food requirements are that a male must capture 5-8.3 medium-sized fish (total 1250 g or 1125 kcal) to sustain himself, a mate and three young. To support himself when not nesting, a male would require about two fish per day. The maximum rate would have to be sustained for the 60-day Chesapeake nestling period during May and June, about half that during the 55 days of courtship-incubation in March and April, and about a third the maximum rate in the July-August fledging period and the February-April and August-October migratory periods.

Nest Site Requirements

Nest sites are important in providing previous nesters and newly recruited nesters with places to reproduce successfully. Additionally, an ample supply of potential nest sites promotes breeding at an earlier age which increases population stability. The younger a bird can reproduce, the more productive years are available in its life span and the less each pair has to contribute towards the produc-

tivity rate required for population stability. Nest sites are also important in distributing nesting ospreys into new areas.^{9,32,35,36,40,45}

A 1973 survey of the nesting population found nearly two-thirds of Chesapeake ospreys were nesting offshore on artificial structures erected to support water-oriented industries. It found 31.7% of the nests in trees, 28.7% on offshore hunting blinds, 21.8% on marine navigational aids, and 17.8% on artificial structures, mostly offshore. The transition from ancestral, tree sites to artificial nest sites has taken place over the past several decades following increases in predatory raccoon populations, shoreline development (disturbance, destruction of trees), and support for water-related activities (piers, navigational aids, hunting blinds). Offshore structures offer protection from most terrestrial predators and human activities, permit rapid detection of danger and quick escape, and place the birds nearer their food supply. The continued availability of Chesapeake osprey nest sites depends largely upon the erection of suitable artificial structures and tolerance of their operators. Ideally a suitable nest site should be located in an area of minimal exposure to human activities, and these activities should be present before ospreys commence nesting in late March to early April. Habituation to human disturbance is essential if nesting pairs are to achieve their reproductive potential.^{9,16,30}

SPECIAL PROBLEMS

Human Disturbance

Osprey will flush from their nests upon close approach by humans, spending valuable energy circling, screaming and making mock attacks. Absence from the nest may endanger the eggs or nestlings through exposure to sun, wind, rain, cold, missed feeding, or even cause the loss of the egg or young to a predator. Disturbance by humans may result in higher food demands, lowered productivity, emigration from the area, and a decrease in the local population. Several studies attribute nest abandonment, or egg and nestling losses, directly to human activities near nests. The most susceptible nests are those in undisturbed locations that are suddenly interrupted by human activities later in the nesting season. The influence of disturbance on reproductive success becomes more pronounced each year as human populations and development increase in the Chesapeake Bay area. The influence of human disturbance on ospreys is an area which needs further study.^{1,3,4,24,25,30,42,43,44,57,60}

Ospreys often select artificial structures such as marine navigational sites, electric cable support structures, water towers, and chimneys. Nesting osprey can impede the function or original purpose of these structures, and in the past operators of the structure often removed nests. Conflicts can be avoided, however. Some agencies and companies such as electric power companies, the U.S. Navy,

and the U.S. Coast Guard have modified their structures to accommodate both the osprey's need for nest sites and the need for a functioning structure. Private individuals who own shoreline property in many cases have provided platforms suitable for osprey nests. The osprey is becoming increasingly dependent on artificial structures because of the loss of natural nest sites to shoreline development.^{1,19,29,36,37,40,41,43,44,45,46,48,49,59,61,63}

Toxic Contamination

In the past, high concentrations of various organochlorine compounds were detected in Chesapeake osprey eggs and tissues. Residues of DDT and its metabolites, PCB and dieldrin were most prevalent.

The DDT metabolite DDE is known to reduce shell thickness of eggs. It also has been shown to lower pore density during shell formation, which reduces evaporative exchange through the shell, thereby placing the embryo at risk regardless of shell thinning. Chesapeake shell thickness reduction ranged up to 35% during the 1960's and 1970's; however, eggs in most tributaries were thinned only 10-20%. Eggshells thinned > 15% are likely to break. Damaged and broken eggshells were largely responsible for poor reproductive success and population declines noted in many parts of North America in the 1960's. Dieldrin, DDT, and some of the other organochlorines have been banned for use in the United States since the early 1970's, but they are still used indiscriminately in tropical regions where ospreys spend several months of each year. See this volume, EFFECTS OF CONTAMINANTS ON BIRDS, for an evaluation of the effects of toxic contaminants.^{7,32,43,52,67}

Weather

Adverse weather can affect local nest success in several ways but generally does not limit populations. Wind or ice destroyed 12% of the terrestrial and offshore Chesapeake nests in 1966-79 studies, with annual attrition sometimes reaching 43%. Some birds returning to these sites were forced to delay nesting, emigrate, or to occupy a less desirable site nearby. Weather during the nesting season was responsible for the loss of 5% of the 1761 nests studied, along with 106 eggs and 65 nestlings. Wind and rain caused 50% of the weather-related egg losses and 66% of the nestling losses. Other losses occurred at sites that collapsed after being weakened by weather. Annual mortality can be increased by a single storm such as tropical storm Agnes in 1972, which killed 18% of all the nestlings produced. Cloudy conditions with rippled surface water lowers fishing success for ospreys, which could jeopardize hungry nestlings. The effect of weather on osprey mortality, nest success, and population stability may need further consideration and investigation.^{12,40,41,42,43,44}

Disease

Pathogenic bacteria of the genera *Actinobacillus*, *Staphylococcus*, and *Streptococcus* have been identified as the agents of pneumonia diagnosed in osprey mortality studies. Anemia, nephritis, cloacal obstruction, peritonitis, and stomach ulcer have also been diagnosed in the death of ospreys. Emaciation, gangrene, enlarged spleen, necrosis, prolapsed oviduct, mycosis, pericarditis, and myocarditis are largely secondary mortality factors associated with food stress or major trauma of disease, injury, or poisoning. Bone and joint sarcomas and limb abnormalities found in ospreys are usually the result of skeletal and support tissue injury, especially among nestlings and fledglings, although some of these abnormalities could result from exposure to contaminants. Flukes found in the ventriculus of one Chesapeake osprey have been identified as *Ribeiroia ondatrae*, roundworms collected from alimentary tract organs, and body lice from the plumage of other ospreys are unidentified. Most disease-related deaths go undiagnosed, indicating the need for more comprehensive evaluation and identification of causative agents, and assessment of disease-related mortality on the population.^{43,62,65,66}

Shooting and Other Intentional Acts

Shooting of osprey occurs but the extent of this problem is difficult to assess. Shooting usually takes place over water or in remote areas where killed birds quickly sink or are difficult to detect. Shootings generally are kept secret and precautionary burial or disposal can make detection difficult. Shootings are likely to take place in sparsely populated areas where roads pass close to terrestrial nest sites, and over ponds and fish hatcheries. Shooting birds on the nest may occasionally occur in more public areas. Many studies suggest that shooting on the breeding grounds is a far more serious mortality factor than generally believed.^{3,8,11,32,38,47,50,61}

Malicious destruction of nests and stealing large nestlings for pets occurs in nests on structures low over the water. Indiscriminate removal of pre-fledged young by wildlife managers for establishing ospreys in areas where they do not occur could have a maximum population impact where temporal patterns of nestling mortality are not known.^{17,19,37,40,43,47,61,63}

Accidents

Many young and adult ospreys are accidentally killed each year by electrocution on utility structures, nest fire, and striking overhead cables. Others starve while tangled in discarded monofilament fishing line or drown in fish nets. Fatalities also are caused by dogs, birds trapped inside duck blinds, automobiles, aircraft, sailboat masts, and guy wires on communication towers.^{32,65,66}

RECOMMENDATIONS

Nest sites

Erection and maintenance of offshore artificial nest structures, located in areas of minimal human activities, are recommended to enhance the availability of suitable nest sites. Structures should be in place before ospreys commence nesting in March or early April. Nest structures should be more than 50 meters offshore from the low tide shoreline, or over 150 meters offshore if the adjacent shoreline is wooded. These distances will discourage predation by raccoons and great horned owls. Nests also should be more than three meters above the high tide level to preclude viewing nest contents from a small boat.

Management

Management actions should include enforcement of existing laws protecting ospreys. Agencies, companies, and private individuals whose activities affect nesting ospreys should be guided by policies that protect birds and their nests. A public awareness program could educate concerned citizens about the ospreys' need for safe nest sites and their vulnerability to human disturbance and environmental contaminants.

Periodic monitoring of nest success and analysis of eggs and body tissues for toxic chemicals and metals would allow an immediate response to any contamination. Continued monitoring of ospreys is recommended in view of the long half-life and toxic effects of organochlorine compounds and the ospreys' exposure to toxins in some wintering areas. Construction of artificial nest sites, decreasing human activities near nests, and assuring adequate prey base are especially important to maintain the current population as well as aid recovery in the years following a weather-related disaster.

Research

Important subjects that need research include osprey preferred prey type, size, abundance, ecology, and nutritional value; the influence of human disturbance on reproductive success; the identification of parasites and agents responsible for diseases and stress-related mortality; mortality rates of specific age and sex classes to improve estimates of productivity rates required to maintain population stability; and foraging efficiency and energy budgets.

CONCLUSION

The Chesapeake Bay osprey population has shown an increase since the early 1970's, largely due to the banning of DDT and the osprey's adaptability to artificial nest structures. Many anthropogenic activities influence Chesapeake Bay ospreys, including the removal of active nests from structures serving humans, toxic contamina-

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tion of the environment, shooting, pollution of Bay waters, over-harvesting of fish, and annoyance by humans. Most of these problems can be minimized by increasing public awareness of osprey problems, enforcing laws protecting ospreys, developing and implementing management actions for ospreys, and providing management assistance to businesses and individuals adversely affected by osprey activities. Resolving problems related to chemical contaminants, deteriorating water quality, and

dwindling fish populations can be achieved only through more far-reaching efforts involving Chesapeake Bay clean-up programs and controls on pollution and aquatic resource harvesting.

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OSPREY

Table 1. Daily rate of male fish deliveries to Osprey mate and nestlings.

Location	Eggs	No. Fish Deliveries/Brood Size				With Nestings
		1	2	3	4	
Florida Bay, Fla. ³¹						4.3
Orange Lake, Fla. ²	3.0					4.0
Newman's Lake, Fla. ²	2.5					3.5
Sante Fe Lake, Fla. ²	4.0					4.2
Chesapeake Bay, Va. ⁵⁴						8.3
Long Is. Sound, N.Y. ³¹						5-8.2
Flathead Lake, Mont. ²⁰		3.4	2.7	4.6		
Cascade Lake, Idaho ⁶⁰			4.6	5.6		
Eagle Lake, Cal. ²⁰		3.0	3.9	4.6	5.0	
Humboldt Bay, Cal. ²³	3.4		6.6			

Table 2. Average length and weight of osprey prey species.

Location	Species	% Composition	Length (cm)			Weight (g)	
			mean	range	n	mean	n
Newnan's Lake, north Fla. 1972 ²⁶	Threadfin shad	70					
	Gizzard shad	4					
	Sunfish		18	7.5 - 35	34		
	Black crappie	26					
	Largemouth bass unidentified						
Florida Bay, Fla. 1978-79 ³¹	unidentified					190±13 ^a	
Long Is. Sound, NY 1978-79 ³¹	Winter flounder	50				172±11 ^a	
	Winter flounder	50				183±10	
Halifax, coastal Nova Scotia 1981 ¹⁰	Alewife		24±3 ^b		46	220±82 ^b	46
	Smelt		19±4		32	54±27	32
	Winter flounder		18±7		31	102±114	31
	Pollock		37±6		27	630±250	27
North-central Minnesota Lakes 1966-71 ⁵	Bluegill		12.8		76	51	76
	Black crappie		17.2		67	82	67
	Yellow perch		15.3		28	37	28
	Largemouth bass		21.9		22	144	22
	Pumpkinseed		13.2		9	54	9
	White crappie		18.3		7	77	7
	Northern redhorse		27.6		4	612	4
Yellowstone Lake, northwest Wyoming 1973-74 ⁵⁶	Cutthroat trout	93	28	10 - 40	116		
	Longnose sucker	7	28				
Cascade Reservoir, west-central Idaho 1978-79 ⁶⁰	Brown bullhead	28					
	Northern squawfish	24					
	Salmonids	20		89% between			
	Lg.-scale sucker	11		11 - 30	152		
	unidentified	11					
Humboldt Bay, northern California 1972 ⁵⁸	Yellow perch	6					
	Surf perch	63					
	unidentified	24					
	Anchovies	3		18 - 23	211		
	Silversides	2					
	Herrings	2					
	Sculpins	1					

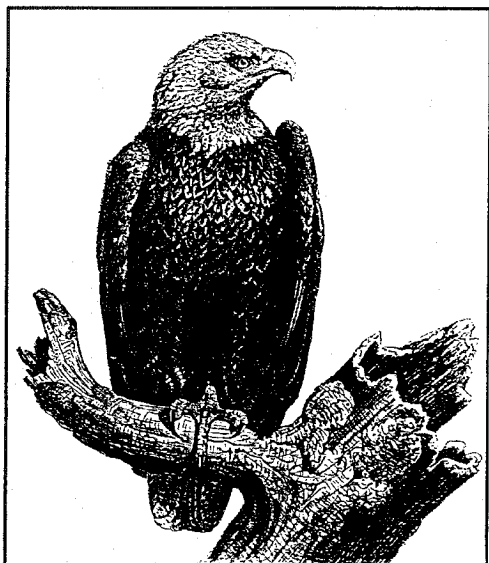
a) mean ± S.E.

b) mean ± S.D.

BALD EAGLE

Haliaeetus leucocephalus

James D. Fraser¹, David A. Buehler¹, Glenn D. Therres² and Janis K. D. Seegar³



The Chesapeake Bay may once have provided habitat for as many as three thousand pairs of breeding bald eagles and for thousands of subadult and migrant birds. The population has declined dramatically over the past three centuries due to habitat destruction, persecution, and contamination by DDT and other chemicals, reaching a low of 80-90 breeding pairs in 1970. After DDT was banned in 1972, the population began to increase. In 1989, 185 pairs of eagles nested in Maryland and Virginia.

Eagles require large trees for nesting, roosting, and perching. These trees must be in areas with limited human activity. Bald eagles are opportunistic predator-scavengers, consuming many different prey species. They take fish when they are available, but shift to waterfowl and mammals when fish are scarce.

The long-term survival of the bald eagle on Chesapeake Bay will be determined by the management of shoreline habitat. The very rapid rate of shoreline development, if unchecked, will eliminate

most large undisturbed forest blocks in the next 50-100 years and will lead to a decline and perhaps extirpation of the species from the Chesapeake Bay area. This can be avoided if a series of shoreline refuges is created. Adequate fish and waterfowl populations also will be required to sustain the species in the future.

INTRODUCTION

The bald eagle has long been special to Americans.²⁷ It became the national symbol in 1782 because of its regal appearance and because, as the only sea eagle native to this continent, it is uniquely American. A carnivore that is sensitive to environmental changes, the eagle is also an indicator of the health of our beleaguered coastal ecosystems. The decline of the Chesapeake's eagle population (which may once have numbered in the thousands) to less than 100 pairs by 1970 is a clear indication of the degradation of the Chesapeake ecosystem.

The species is now recovering from the widespread nesting failures caused by DDT, but its future survival is endangered by development of the Bay's shoreline habitat. The fate of the eagle on Chesapeake Bay will mirror the fate of the shoreline forests which once sus-

tained native Americans and European settlers, and which still protect the Bay's watershed and provide habitat for wildlife and enjoyment for people.

BACKGROUND

The bald eagle is found near large bodies of water throughout North America, from central Alaska and northern Canada to northern Mexico, Baja California, the Gulf coast, and Southern Florida.⁵ Two subspecies are recognized, based on size. In the eastern United States, the larger subspecies (*H.l. alascanus*) breeds from Maryland north, while the southern subspecies (*H.l. leucocephalus*) breeds from Virginia south. The demarcation of the breeding range of the two subspecies is arbitrary⁴ and some authorities question the validity of the subspecific designations.²

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Eagle breeding sites are located throughout the Chesapeake shoreline, generally within 1 km of the water^{3,26} in sparsely developed or undeveloped areas. Nesting concentrations are greatest along the Potomac and Rappahannock Rivers and in Dorchester County Maryland, and lowest in the vicinity of urbanized areas like Baltimore, Washington, and Norfolk (Map Appendix). Locally hatched subadult eagles are similarly distributed. Northern and southern migrants tend to be more clumped into concentration areas⁹ although these areas are also used by local birds.

Summer concentration areas include the Aberdeen Proving Ground, Maryland; Caledon State Park near Owens, Virginia; and the James River from Windmill Point to Tar Bay. Winter areas include the Aberdeen Proving Ground; Mason Neck National Wildlife Refuge; the Blackwater National Wildlife Refuge and Fishing Bay Wildlife Management Area and vicinity; the Rappahannock River near Fredricksburg and Champlain; the James river on Presquile National Wildlife Refuge; the Chickahominy River; and the Pocomoke River near Rehobeth, Maryland. A small fall concentration area is located on the Susquehanna River just below the Conowingo Dam (Map Appendix).^{9,12}

Eagle densities on the pristine Chesapeake are unknown. However, given the high productivity of the Chesapeake prior to European settlement, it may be reasonable to assume that they were similar to densities found in undeveloped Alaska today. Applying Alaskan densities^{25,35} to the 13,000 km of Chesapeake shoreline,²⁹ suggests that the Chesapeake breeding population before European settlement may have exceeded 3000 pairs.

Although records are lacking, the eagle population undoubtedly declined substantially in the 17th and 18th centuries. During this period, much of the original forest was cleared for agriculture, and many nesting, perching and roosting sites were no doubt destroyed. Moreover, eagles, like other predators, were routinely persecuted.^{6,22} Thus, by the end of the 19th century, a number of authorities were expressing concern about the eagle's future.^{7,8,34}

In the late 1940's a new problem was added to those of habitat destruction and shooting: DDT, an insecticide that entered aquatic food webs and caused eagles and other fish-eating and predatory birds to lay thin-shelled eggs.⁴³ As a result, although Chesapeake eagle pairs in 1936 produced, on average, 1.6 young per nesting attempt, by 1962 production had declined to 0.2 young produced per pair.³⁸ This low reproduction, coupled with increased mortality due to other contaminants (notably dieldrin and kepone) and from continued shooting, caused the eagle population to decline to a number even below the levels dictated by the diminishing habitat. By one estimate, the

breeding population had decreased to 80-90 pairs by 1970.¹

Following the end of commercial DDT use in the early 1970's, eagle reproduction began to increase, and by 1985 productivity had returned to pre-DDT levels. Mortality due to shooting may also have declined. The population began to grow. In 1989, 185 pairs of eagles laid eggs in Maryland and Virginia.^{12,38} Although this increase in the population is a good sign, the eagle is not out of danger in the region because its habitat is rapidly being destroyed.

LIFE HISTORY

Chesapeake Bay adult eagles generally remain in their nesting territories throughout the year,⁹ and may be seen repairing nests or building new nests during any month of the year.^{19,38} During the winter, however, attention to the nest increases in preparation for the breeding season. Egg laying takes place in January through March, with a peak in February.³⁸ Typically one to three eggs are laid, but there are three unpublished records of Chesapeake clutches containing four eggs and three records of five-egg clutches. In addition, we observed one brood of four chicks in 1986. Incubation lasts 35 days.²⁴

Chicks typically leave the nest at 10-12 weeks of age.¹⁹ However, occasionally young are blown out or fall out prior to fledging. These young are cared for by their parents and many survive. Thus, Chesapeake young leave their nests from May through July. The young rely on their parents for a number of weeks after their first flights, but gradually learn to hunt and begin to spend more time away from the nest. By winter, their movements are similar to other subadult birds.

Eagles do not attain the adult's white head and tail until they are four years old;³¹ they very rarely establish breeding territories before then. Birds in subadult plumage move among undeveloped forested habitats throughout the year, depending in part upon prey availability. Chesapeake-hatched nonbreeders tend to move toward the northern Bay in summer and toward the south in winter. Although they occasionally stray as far north as Maine during the summer, and as far south as North Carolina during the winter, locally reared birds spend most of their lives on or near the Chesapeake.^{9,39}

In addition to providing year-round habitat for locally reared eagles, Chesapeake Bay provides key habitat for migrating eagles as well. Eagles from Maine, New Brunswick, and other northern areas winter on the Bay from November to April. Eagles from Florida and other southern states summer on the Bay from April to October.⁹ A few migrants may linger beyond these general time periods. We observed one radio-tagged Florida bird on the Chesapeake in January, for example.

During the summer, eagles are primarily piscivorous. They forage most intensely at first light, but will take prey at any time of day. Most hunting is done from a perch and most fish are captured in shallow water, where fish density is greatest.³³ In winter, when fish availability declines in parts of the Bay, eagles switch to waterfowl and other species, probably taken mostly as carrion.³³

Eagles roost solitarily or communally throughout the year. In one study on the northern Chesapeake, communal roosting was least common during the summer and most common during the fall.¹¹

ECOLOGICAL ROLE

Bald eagles are opportunistic predator-scavengers, taking many species of fish, birds and mammals.^{18,33} They prefer fish taken alive or dead, but turn to waterfowl, white-tailed deer, and other species during the winter when fish are scarce. Studies on the northern Chesapeake suggest that eagles may prey on different fish species in proportion to their availability. Gizzard shad, channel catfish, Atlantic menhaden, and white perch were the most commonly identified eagle prey species and were also the most common species caught in gillnets.³³ American eels and yellow perch were also common prey for eagles. Similarly, Atlantic menhaden and American eels were the species most commonly delivered to young in nests on the Potomac and Rappahannock Rivers.⁴¹ Carp were commonly found at nests during banding operations,¹⁸ but this may reflect the long life of the remains of this species³³ rather than a feeding preference by eagles. Gizzard shad may be a particularly important prey species because, unlike many others, it is frequently available in winter.³³

In November on the northern Bay, waterfowl numbers increase, and hunting of them increases the availability of crippled and dead waterfowl. At the same time fish availability declines. Probably in response to this change, eagle use of fish declines and use of waterfowl, primarily mallards and Canada geese, increases.^{28,33} Scavenging of white-tailed deer and other mammals also increases in winter. As waterfowl numbers decrease and fish become more abundant after January, eagle use of birds and mammals declines, and is infrequent by May.

In addition to the fish and waterfowl that make up most of the eagle's diet, a variety of other species may be taken including herons, hawks, passerine birds, gulls, raccoons, muskrats, rabbits, turtles, and many others. Some of these are undoubtedly taken as carrion; others are likely pirated from other predatory birds.^{18,33}

HABITAT REQUIREMENTS

Water Quality

Changes in water quality affect bald eagles chiefly through their impact on prey species. However, because bald eagles are opportunistic in their choice of prey, a decline in a particular prey species may be offset by increases in other prey. Thus, maintaining water quality standards that provide for a high biomass of a variety of species will benefit the bald eagle. Maintaining conditions suitable for gizzard shad may be particularly important in the northern bay, since this appears to be the chief fish prey during winter months when other species are scarce.³³

Structural Habitat

Ideal eagle habitat consists of mature shoreline forests with scattered openings and little human use, adjacent to water with abundant fish and waterfowl (Table 1). Such habitat must contain adequate nesting, roosting, and perching sites.

Nesting Sites

Most eagle nests on the Chesapeake (> 60%) are in loblolly pines. A variety of other tree species are used, including shortleaf pine, Virginia pine, white oak, chestnut oak, northern red oak, swamp white oak, southern red oak, willow oak, North American tuliptree, American beech, bitternut hickory, American sycamore, and American sweetgum. None of these species (other than loblolly pine) accounts for more than 10% of the nesting sites.^{3,17,26}

Nest trees are typically large super-canopy trees. Mean nest tree heights in Virginia and Maryland were 30 m and 23 m respectively, and diameters were 57 cm and 62 cm.^{3,26} This compares with heights and diameters of randomly selected trees of 17 m and 39 cm, respectively, suggesting that trees large enough for eagles are uncommon on the Chesapeake (only trees larger than 20 cm were included in the random tree sample).¹¹

Eagles usually choose nest sites within a kilometer of water, in open or broken mature forested habitat.^{3,26}

Roosting Sites

Like nest trees, roost trees differ from average trees near the shoreline. In one study on the northern Chesapeake, the mean diameter of roost trees was 74 cm compared to the 39 cm diameter of randomly selected trees. All roosts were in forest blocks greater than 43 ha; more than 40 % were in a single 5000 ha forest block.¹¹ In contrast, 48% of forest blocks on the study area were smaller than 43 ha. Roosts are typically located in areas with little or no human development and adjacent to good foraging habitat. Oaks, beeches, and North American tuliptrees were used most frequently for roosting in the northern Chesapeake,¹¹ but other species including loblolly pines are used elsewhere on the Bay.^{11,15} Roost trees are probably selected on the

BALD EAGLE

basis of size, habitat, location and branch configuration rather than by species.

Perching Sites

Eagles spend most of the daylight hours perched. Most hunting is done from a perch and most strikes at fish are made within 100 m of the shoreline. Thus, widely distributed suitable perches near foraging areas may be especially important to bald eagles.³³ Like roosting and nesting trees, perching trees are much larger than the average shoreline tree. In one study on the northern Chesapeake, perch trees averaged 53 cm in diameter, compared to an average of 34 cm for trees randomly selected from perching areas.¹³

SPECIAL PROBLEMS

Shoreline Development and Human Disturbance

The most pressing problem facing the Chesapeake bald eagle is the conversion of shoreline forest to housing developments, marinas, and other types of human habitat. This process removes trees used by eagles for nesting, roosting, and perching and increases encounters between eagles and people. These encounters can alter eagle behavior, often reducing or eliminating eagle use of some areas.^{10,21,30,32,37}

For example, Chesapeake eagles generally avoid buildings and roads when choosing nest sites.³ Jaffee²⁶ reported that inactive nests were closer to the water than active nests. Because human activity near the shoreline has been increasing, this pattern of nest selection suggests that eagles are moving away from the water in response to human activities along the shoreline. This is consistent with observations in Minnesota where recently discovered nests were farther from the shoreline than older nests.²¹ Jaffee²⁶ characterized human activity at 33 of the 40 nests studied as "light", which is consistent with the observation that eagles appear to avoid human developments when choosing nest sites.

Even when nests are far from developments, human activities can disrupt normal eagle behavior. Areas used by eagles for perching are almost always in undeveloped or very lightly developed areas. Areas with more than one building per hectare are almost never used.¹⁰ Similarly, boat traffic can disturb eagles and reduce eagle use of the shoreline.^{10,30,42}

It is not known how far from the shore human activity should be to avoid disturbing eagle shoreline use, but analyses to date suggest that houses as much as 500 meters from the water may discourage eagle use.¹⁰ Similarly, studies on the Columbia River in Oregon suggest that human activity 800 meters from traditional perches can reduce eagle use.³²

Most nests and roosts are on private lands¹⁷ and private property along the Chesapeake is being developed rapidly. The 2020 Report,²³ a study done for the Chesapeake Bay Executive Council, predicted a 73% increase in the amount of developed area in the Maryland portion of the Chesapeake Bay watershed and an 80% increase in the developed area in the Virginia portion of the watershed by the year 2020. Much of this development will take place on the private land that eagles use. Thus we expect the eagle population to continue to increase to the level the natural habitat can support, and then decrease as forested shoreline is developed. If shoreline development continues at the rates predicted in the 2020 Report, most eagle habitat on the Chesapeake will be gone in 50-100 years, and the substantially reduced eagle population will be confined to the few remaining islands of habitat in the public domain.

In Maryland, the Chesapeake Bay Critical Area Protection Program¹⁴ provides for certain sections of shoreline to be set aside as Resource Conservation Areas, including wildlife habitat areas.⁴⁰ Appropriate protection of bald eagle nest sites are mandated by this program,⁴⁰ but the extent of that protection may not be sufficient to protect the eagle population. The effectiveness of the program needs to be evaluated, but at present we suspect that many such areas may be too small to be of much help. For example, the general guidelines call for forested buffers 100 feet wide along tidal shorelines, whereas eagles need larger undeveloped areas. Similarly, the 100-foot buffers provided under Virginia's Chesapeake Bay Preservation Act will provide little protection.

A smaller scale approach to protecting habitat is to create "buffer zones" around key habitat components such as nest sites and roost sites. Human activity that could disturb eagles or degrade eagle habitat (e.g., construction or extensive land clearing) are excluded from these zones.

Currently a quarter-mile-radius buffer exists around nest sites in the Chesapeake region, with recommendations for differing restrictions in three zones (0-100 m, 100-200 m, and 200-400 m) within the buffer.¹⁶ Recommended restrictions on human activities are greatest during the breeding season. Although this buffer scheme, coupled with adequate vegetative screening may be sufficient to protect some nesting eagles, reports that eagles may be disturbed by human activities as distant as 800 meters^{10,20,32} indicate that the system should be carefully evaluated by field experimentation.

Despite the widespread use of nest buffers, it is clear that the tiny habitat parcels they provide do not adequately protect foraging habitat used by nesting eagles. Moreover, nest buffers do not protect habitat needed by non-breeding eagles for roosting, perching, and foraging. Long-term survival of the bald eagle on the Chesapeake Bay will

require retention of extensive shoreline forests with large (> 50 cm diameter) trees.

Shooting

Despite an apparent decrease in shooting rates,²⁰ eagles are still being shot. Even fairly low shooting pressure can reduce the population in a slowly reproducing species like the bald eagle.

Contaminants

Although the great threats caused by chlorinated hydrocarbons such as DDT and dieldrin have subsided with the banning of these chemicals, the bald eagle's role as a top carnivore and scavenger makes it vulnerable to ingesting new chemicals that may enter its food chain. Thus it will remain at risk due to such chemicals. The chapter on toxic impacts to birds addresses this issue.

RECOMMENDATIONS

We believe that the following actions are required to ensure the continued viability of the Chesapeake eagle population. Many of these recommendations mirror those in the Chesapeake Region bald eagle recovery plan. Unfortunately, the plan has been incompletely implemented.

Management Recommendations

Establish a System of Eagle Refuges

If bald eagles are to regain their former status as significant members of the Chesapeake ecosystem—indeed, if they are to maintain even their current low numbers—significant areas of shoreline forest will have to be preserved. The optimal size for such sites is unknown, but it is clear that the larger the area, the more effective the refuge. This is true not simply because larger refuges provide more space for eagles, but also because smaller refuges will be more subject to human disturbance from outside the refuge borders. For example, assuming a disturbance distance of 800 meters (and ignoring the effect of vegetative buffers) a square, 4 km² refuge would encompass 400 ha, but would have only 16 ha of disturbance free area (4% of the refuge area), while a square 400 km² refuge encompassing 40,000 ha, would have 36,800 ha of disturbance free area, or 92% of the total area. Ideally, refuges should be adjacent to the Bay or its largest tributaries and should abut shallow waters with good fish and waterfowl populations.

The first priority for protection should be placed on unprotected areas now known to receive substantial eagle use. A second level priority should be placed on undeveloped areas not currently known to receive eagle use, but which, with proper management, could be developed into prime eagle habitat. Deforested agricultural areas adjacent to apparently suitable foraging waters would be good candidates for this category.

Eagle refuges need to be protected by irreversible arrangements. This could include outright land purchase by public agencies, purchase of development rights, or permanent conservation easements. Voluntary agreements with landowners, while a good stop-gap measure, will not likely survive periods of increasing land values and higher tax rates. Shoreline is being developed at a very rapid rate. Thus, creation of shoreline refuges is an urgent need that will require a cooperative effort involving Federal, state, and private entities.

Continue the Current Buffer Zone Policy

Although the current buffer zones are not an adequate substitute for preserving large forest blocks, they do provide some protection for significant habitat elements. It seems unlikely that enough habitat will be protected in large reserves to guarantee the viability of the population. Thus, buffer zones around key areas on land being managed primarily for other purposes should remain a part of the Chesapeake eagle management strategy for the foreseeable future.

Inventory All Federal Lands For Eagle Use, and Review the Eagle Management Plans For These Areas

The Endangered Species Act gives Federal agencies special responsibilities for conserving threatened and endangered species. Each Federal property should have an eagle management plan that ensures protection of eagles and eagle habitat.

Continue To Encourage Landowners To Manage Their Properties To Benefit Eagles

Where it is not possible to effect permanent, binding protection of habitat, landowners should be encouraged to conserve eagles voluntarily. The landowners guide¹⁶ used in the past as a key reference in this process should be updated to reflect recent findings about bald eagle responses to human activities.

Conserve An Uncontaminated Prey Base

If the efforts to conserve uncontaminated populations of fish and bird species outlined elsewhere in this volume are successfully implemented, little else should be necessary to provide adequate prey for bald eagles. Conservation of frequently used prey species such as the gizzard shad, Atlantic menhaden, channel catfish, white perch, American eel, mallard, Canada goose and white-tailed deer may provide the greatest benefit to the bald eagle.

Educate The Public About Threats To Eagles And Shoreline Habitats

Continued effort should be made to educate the general public about the impact of land development, shooting, and other human activity on Bay bald eagles. Only a knowledgeable public will be likely to support the expen-

sive habitat conservation efforts required to secure the bald eagle's future on Chesapeake Bay.

Continue Enforcement Efforts

Although shooting eagles has declined, some shooting and intentional poisoning still occur. Continued enforcement is needed to deter such acts.

Research Recommendations

Inventory Key Habitats

Although nest locations and some concentration areas are well known, other concentration areas are still being discovered. A systematic aerial survey of the shoreline should be conducted to determine if areas are being overlooked. At a minimum, early-morning surveys during the late summer and mid-winter population peaks^{9,42} should be undertaken. Alternatively, radio-telemetry studies can delineate the most important congregation areas.

Creating refuges will also require inventory of the undeveloped portions of the Chesapeake shoreline, whether or not they are currently used by eagles. This inventory should include a description of the habitat characteristics and development status of those areas and an analysis of the effect of Maryland's Critical Area Program and Virginia's Chesapeake Bay Preservation Act on eagle habitat. Existing habitat, development and zoning characteristics should be included in a geographic information system data base to facilitate decision-making, research and monitoring of eagle habitat status. Additional research should be conducted to develop a system to rank existing and potential habitat by its potential to aid long-term population survival. (The initiation of habitat acquisition should begin immediately, however. There are substantial unprotected parcels of obvious great value to the eagle population.)

Determine Shoreline Requirements of Nesting Eagles

A study of foraging habitat requirements of territorial eagles and their offspring should be initiated. Information from such a study would allow buffer zone prescriptions to be accompanied by prescriptions for managing the shoreline habitat used for perching, foraging, and roosting. It would also help determine whether relaxation of restrictions near nests in the non-breeding season is war-

ranted, given the fact that adults remain on territory throughout the year.

Evaluate the Efficacy of Current Buffer Zones

It is unclear if the current buffer zones are large enough to protect eagles adequately. These should be evaluated by studying eagle habitat use in response to experimental disturbances.

Conduct Population Viability Analyses

Population viability analyses³⁶ should be conducted to determine the desirable number and distribution of eagle refuges. Until enough habitat has been irrevocably protected to ensure long-term viability of the Chesapeake population, all known habitat areas should be vigorously protected.

Determine the Factors Regulating Eagle Distribution and Abundance

Currently the Chesapeake population, released from the impacts of DDT which had been limiting eagle numbers, is increasing rapidly. That increase cannot continue indefinitely. Within suitable habitat, the size of the eagle population may be limited by the number of suitable nest trees, by prey availability, or by some other factors. Effective management of the eagle population at that stage will require an understanding of the factors that regulate the population numbers.

CONCLUSION

The bald eagle, much reduced from former numbers by habitat destruction, shooting, and contamination, is enjoying an increase following a decline in DDT in its food web. This population increase will soon be reversed as the shoreline habitat required by the eagle is converted to housing developments, shopping malls, and industrial sites. Only immediate and decisive action to preserve habitat will prevent this ultimate decline.

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Table 1 Habitat requirements for bald eagle.

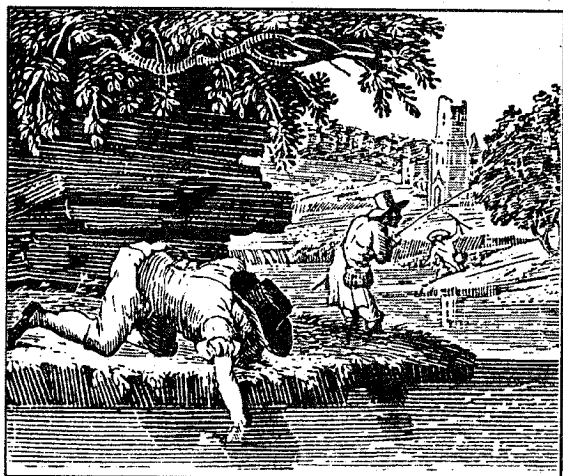
Forested Shoreline	yes
Diameter of dominant trees	≥50 cm
Height of dominant trees	≥19 m
Minimum distance, roosts to human activity	800 m ^a
Minimum distance, nests to human activity	400 m ^b

^aBased on reported disturbance distances. Distances may vary depending on activities within the site of perched eagles and other factors. Details for specific sites should be worked out with the state wildlife agencies and the U. S. Fish and Wildlife Service.

^bBased on the typical outer buffers in use on the Chesapeake Bay at present. Typically greater restrictions on human activity are required in inner sub-zones. Site-specific details should be discussed with the state wildlife agency or the U. S. Fish and Wildlife Service.

EFFECTS OF CONTAMINANTS ON FISH AND SHELLFISH

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A variety of factors influence the effects of toxic contaminants on fish and shellfish, including the sensitivity of species, their life stages, and the inherent biological activity of the contaminants. Environmental exposure is influenced by species' life histories and the persistence, mobility and bioaccumulation potential of contaminants. Toxicity is modified by interactions with the physical, chemical, and biological components of the environment, which in turn govern the transformations, movement and accumulation of contaminants.

Monitoring of toxic substances in Chesapeake Bay has not, as a rule, been coordinated with investigations into effects of toxicants on commercially and recreationally important species. Toxicity information is limited for most of the target species, and virtually absent for some. The bulk of

information comes from laboratory toxicity studies of single chemicals. These tests can provide data on the relative toxicity of chemicals, or relative sensitivity of species, but may not be reliable predictors of environmental effects.

Documented effects of toxicants on Chesapeake Bay fish and shellfish include (1) accumulation of measurable tissue burdens of pesticides, polychlorinated biphenyls (PCB), polynuclear aromatic hydrocarbons (PAH), and heavy metals; (2) development of lesions, deformities, and tumors associated with a few severely contaminated habitats; and (3) high mortality rates of anadromous fish larvae associated with potentially toxic mixtures of contaminants (e.g., aluminum, cadmium, copper, lead, chlordane) in combination with other undesirable water quality conditions in spawning and nursery areas.

Problems of toxicity in the Bay ecosystem require integrated approaches that address multiple chemical and species interactions, and focus on appropriate toxicological endpoints. Protection of fish and shellfish, their prey, and their consumers, from the harmful effects of toxic contaminants will require broad-based, regional strategies to reduce contaminant loads to the Bay and its tributaries.

INTRODUCTION

The Chesapeake Bay Program has been working over the past several years to define the bounds of water quality and habitat conditions within which the Bay's fish and shellfish, along with other living resources, can survive and reproduce. There are no simple solutions to the

problems. There are numerous Bay-dependent species of ecological, commercial, or recreational importance. Thousands of potentially harmful substances enter the Bay from a large array of point and non-point sources. There are thousands of square kilometers of the estuary and its watershed to evaluate and monitor. Yet the most important connections between contaminant exposures and hazards to living resources must be found and inter-

preted in ways that will lead to better management of Bay water quality and protection of living resources.

Fish and shellfish usually are not victims of intentional poisoning. Except for planned uses in lake and pond management and research, the anthropogenic substances that harm living resources are wastes or by-products from industry, agriculture, transportation, and domestic activities. Organisms are exposed to toxicants in their natural habitats because these wastes are poorly managed, through ignorance, carelessness, or economic expedience.

The Cheapeake Bay Program has adopted a regional strategy for reducing loads of toxic substances to the Bay.² The strategy, a commitment of the 1987 Bay Agreement, was necessary because it was recognized that actions to reduce the impacts of toxic contaminants could not be entirely effective on a local, or even state-wide basis. The current restrictions on the use of tributyltin (TBT) paints on recreational vessels are an example of how states can act in concert to address an environmental threat. Maryland and Virginia, by cooperative action, achieved effective control of TBT in the Bay soon after the threat to aquatic life was recognized. Their actions probably hastened the Federal response to the problem.

The objectives of this chapter are: (1) to provide an overview of the ecological toxicity problem as it relates to Chesapeake Bay fish and shellfish; (2) to summarize available toxicity data for Chesapeake Bay target species (we have applied the Chesapeake Bay Program's Toxics of Concern List¹ to narrow the field to a manageable subset of contaminants); and (3) to highlight some important considerations relevant to habitat requirements and needs for additional data.

FACTORS AFFECTING TOXICITY

In the wild, toxicological effects of contaminants are a function of the combined exposure to all contaminants from all sources and the interactions of contaminants with environmental factors, including the organisms themselves. The *sensitivity* of various species to toxicants can be related to physiological species differences and life stage. The *hazard* of a chemical is related to the chemical's inherent toxicity, persistence, bioaccumulation potential, metabolic by-products, and mobility in environmental media. *Exposure* is influenced by characteristics of a species (habitat, feeding mode, diet, etc.), the physical and chemical characteristics of the material (solubility, persistence, etc.), and discharge characteristics (concentration, duration, frequency, etc.). All of these factors may be influenced in turn by environmental interactions with temperature, salinity, pH, dissolved oxygen (DO), etc. Contaminants can threaten survival and successful

reproduction, and subsequently lead to ecological damage, depleted populations, and loss of fisheries.

Sensitivity

Eggs and larvae generally are more sensitive to toxicants than juveniles or adults. For example, the 96 h LC₅₀ of CuSO₄ to larval and juvenile striped bass is 100 and 620 µg/L⁻¹, respectively.¹³ The earliest life stages of fish and shellfish are passive or only weakly mobile, lack fully developed sensory systems, and so cannot actively avoid or escape harmful conditions. Eggs and larvae have large surface area to volume ratios. Therefore, relatively high loadings of contaminants can be absorbed, relative to juveniles or adults. Early-stage larvae, particularly of fish, may not have completely impermeable protective coverings (shells and scales), and are subject to direct cellular uptake of contaminants through the body wall. Further, they may lack fully-expressed enzyme systems necessary for efficient detoxification and excretion of contaminants.

Animals that spawn or undergo early development in the ocean are not exposed to pollutants in Chesapeake Bay during their egg and larval stages. Therefore, the concern for marine spawners in the Bay is with the more resistant juveniles and adults. In contrast, resident and anadromous species potentially are exposed throughout their entire life cycles, or at least during the sensitive egg and larval stages. These species face greater risks from toxic substances. It has been observed that most commercially important species which spawn in the Bay or its watershed have reduced stocks relative to historic levels, whereas the abundance of those that spawn outside the Bay generally has been maintained (e.g., blue crab, Atlantic menhaden) or has increased (e.g., spot).¹⁴ The relative impacts of overfishing, habitat loss, and exposure to toxic substances cannot be determined at the present time. Nevertheless, the opposite trends in stocks of resident versus transient species imply that habitat stresses, including toxic contaminants, are limiting factors for resident species.

Hazard

Chesapeake Bay waters contain numerous anthropogenic contaminants. Many of these contaminants are not acutely toxic at low concentrations, and often are beneficial or essential trace micro-nutrients. The classes of substances generally considered as toxicants in natural waters include heavy metals (e.g., lead, cadmium), some light metals (e.g., aluminum, beryllium), metalloids (e.g., arsenic, selenium), halogens (chlorine and bromine), inorganic compounds (e.g., hydrogen sulfide, ammonia), petroleum hydrocarbons, chlorinated hydrocarbons (many insecticides, PCB, etc.), several classes of pesticides, and PAH. Within these generic groups, different substances can have greatly different toxicities when tested under similar conditions. For example, some pesticides and metals (e.g., toxaphene, TBT, mercury) cause acute mortality to fish or shellfish at concentrations on the

order of one part per billion or even less, whereas others (e.g., chromium, atrazine) do not have observable toxic effects at concentrations 10,000 or more times greater. The variation in toxicity is a function of both chemical reactivity and individual species sensitivity. For example, penaeid shrimp are on average 36 times more sensitive to organochlorine pesticides than mysid shrimp.³ Conversely, mysid shrimp are more sensitive than penaeid shrimp to pyrethroids by a factor of 54. Sensitivity to organophosphorus chemicals is species-specific within the two groups.³

Many contaminants are metabolized to some extent by enzyme systems of organisms. These processes include degradation (chemical breakdown) and conjugation (chemical binding) reactions. Metabolic by-products may be more or less toxic than the original substances, or they may be mutagenic (cause genetic damage). Again, the end result depends on the chemical and the species of organism.

Exposure

Exposure is central to the question of environmental toxicity. Extremely toxic chemicals may be relatively harmless if exposures are short, because the organism may not retain them, or the toxic effects are reversible. Other toxicants may have serious chronic effects at environmental concentrations which are not readily detectable by usual analytical procedures, because the toxicants or their effects are cumulative or irreversible.

Exposure of fish and shellfish to toxic contaminants is influenced by how long the substances remain in the habitat and whether substances that are continually delivered to the habitat accumulate more rapidly than they disperse or degrade. Use of some of the most persistent toxicants has been restricted or banned (e.g., DDT, PCB), but the toxic effects of widespread residues of these substances and their breakdown products are still detectable and are expected to be present for many years. Persistence also affects exposure through the potential for bioaccumulation and bioconcentration. Some toxic substances accumulate selectively in certain biological tissues, where they are not readily metabolized or excreted.

The mobility of a chemical is strongly influenced by its solubility in water and its partition coefficient. Many toxicants are selectively adsorbed by small suspended particles which can be ingested by filter-feeding fish and bivalves or are concentrated in organically-rich sediments ingested by deposit feeders. Once removed from the water column by sedimentation, the contaminants are not immediately available to pelagic species, but may become available via the food chain. Highly soluble chemicals tend to remain in the water column and available to organisms there, but also may be dispersed and diluted to insignificant concentrations.

Bottom-feeders may experience higher exposure through the food chain than plankton-feeding species because sediments tend to accumulate many toxic substances. Predatory species may develop high body burdens of persistent chemicals because their prey have accumulated toxicants from the food chain, possibly multiplied through three or more levels. Benthic animals and rooted aquatic plants may be exposed to high levels of toxicants by simple physical contact with sediments which accumulate hydrophobic chemicals.

Interactions

Temperature, salinity, DO, pH, hardness, alkalinity, contaminant combinations, and genetic adaptation are examples of important factors to be considered in evaluating whether a single contaminant is likely to be harmful to individuals or populations of target species. The effects of these interactions on toxicity are both chemical and biological. The question of biological availability can greatly complicate attempts to assess the toxicity of natural waters by chemical measurements. For example, under some conditions, metals form insoluble compounds or non-toxic chemical complexes, whereas under other conditions more toxic forms (usually the dissolved, simple ionic form) predominate.

For a variety of habitat factors (salinity, DO, temperature, etc.) each species and life stage has a definite tolerance range. The toxicity of a chemical will increase or decrease with the degree of stress imposed upon the organism by these other habitat conditions. Near the limits of species tolerance for a given parameter (e.g., salinity), the toxicity of pollutants would be expected to increase, due to physiological stress.

Temperature

Higher temperatures tend to increase both the chemical activity of contaminants and biological sensitivity to them. Interactions of chlorine exposures with temperature and salinity have received considerable research attention. Chlorine (total residual) was 7.5 times more toxic to juvenile alewife at 30°C than at 10°C; see also WHITE PERCH and SPOT, this volume.

Dissolved oxygen

Low DO is a stress factor for fish and shellfish, and is generally thought to exacerbate the effects of toxicants, although evidence of this effect for the target species is scant. Hypoxia can increase the solubility of some toxic metals, making them more available, and can influence the chemical and biological processes which transform toxic organic compounds to more or less toxic forms. We have found no examples reported in this volume of research into the interactions of DO with contaminants.

pH, hardness, alkalinity, salinity

In fresh and weakly brackish waters, low pH can increase the availability and exacerbate the effects of toxic metals, especially on larval fish. Hardness (approximately the sum of dissolved calcium and magnesium) and alkalinity (acid neutralizing capacity contributed by buffering ions such as bicarbonate), can help to protect against the harmful effects of low pH and toxic metals. Salinity has protective effects similar to those of hardness and alkalinity, suggesting that the critical factor may be the ionic strength of the water more than individual ionic constituents. Most of the information on these interactions has been developed for larval striped bass (see STRIPED BASS, this volume). Less than optimum levels of pH, alkalinity, and hardness have been linked to increased metal toxicity and decreased survival of striped bass larvae in the laboratory, in hatcheries, in on-site and *in situ* exposures, and also have been associated with poor year class success (recruitment) in field studies.

Chemical transformations

Chemical transformations of toxicants are common in the aquatic environment. The toxicity of a substance may be modified greatly by changes in its chemical form. These transformations often are strongly influenced by the chemical and physical environment. Gradients of pH, salinity, temperature, light intensity, and DO can affect the form and toxicity of a contaminant. Salinity can influence the speciation and complexation of metals: the LC₅₀ of cadmium to juvenile blue crabs decreases with increasing salinity, from 320 µg/L at 10 ppt to 11,600 µg/L at 30 ppt, probably because of the lower ionic activity of cadmium (greater complexation) at higher salinity. Sulfate salts of metals generally are less toxic than chloride salts due to dissociation kinetics: the striped bass 96 h LC₅₀ is 50 µg/L¹³ for copper chloride, but is 150 µg/L¹³ for copper sulfate.

INTERPRETATION OF DATA**Applicability of toxicity tests (bioassays)**

The bulk of our knowledge of toxic effects to the target species comes from laboratory toxicity tests. Current regulatory bioassay techniques for water quality monitoring were adapted from human-health based assessment techniques. Simple acute lethality bioassays are difficult to evaluate relative to ecosystems with great chemical and biological complexity. Given the multitude of potential exposure scenarios, test chemicals and interactions, the testing program required to generate a data base for each target species, comparable to standard test species data sets, would be prohibitively expensive. Also, the Chesapeake Bay target species are frequently very difficult to culture and to work with in the laboratory. They are often highly susceptible to handling stress, which is partly responsible for the paucity of data on them.

No single chemical or group of chemicals is responsible for toxicity problems in the Bay. Unfortunately, too little research has been done on the effects of multiple contaminants on fish and shellfish to generalize about the interactions of contaminants. Similarly, no single species can be identified as an appropriate sentinel for gauging toxicant effects in the Bay. Regulatory water quality limits and monitoring requirements are based upon the toxicity of chemicals or effluents to standard test species. In some cases, these species are not even natives or residents of the Bay. Indeed, those species which are of direct interest to man frequently are the most poorly investigated in relation to effects of toxicants. However, specific assays with target species of concern may not be required to assess the appropriateness of surrogate species used in environmental monitoring, unless there is reason to believe the target species are particularly sensitive. As an example, it should be noted that striped bass are one of the Bay's most sensitive species to pH depressions.

Environmental stress induced by toxicants should be viewed as one of several density-independent factors that affect the ultimate health of populations. An examination of toxic stress in the Bay must link toxicological responses of test organisms to responses at the population and community levels. A battery of assays, which assess reproduction and recruitment of a spectrum of species, is the most practical approach to environmental assessment of toxicant stress, given the current state of knowledge. For example, the Maryland Department of Natural Resources and the Chesapeake Bay Program currently are conducting a pilot study to test the sensitivity and efficacy of a variety of ambient toxicity bioassay techniques. These assays will require further correlation with community assessments to address habitat impacts, including trophic interactions, for selected target species.

The development of human health bioassays also resulted in a system of biochemical stress indicators which are very sensitive indicators of toxicant exposures, and are predictive of human health problems. There have been limited attempts to evaluate these "biomarkers" in aquatic species. However, scant data on the real world utility of these techniques currently exists. The ecological relevance of biomarkers for aquatic species generally is unknown. The sensitivity of biomarker techniques cannot yet compensate for the degree of extrapolation required to estimate ecosystem effects from evidence of chemical exposure.

Monitoring data

Interpretation of existing data on the occurrence of toxicants in the Bay and the effects of chemicals on biota is complicated by a variety of problems. One problem is the low geographical resolution and spotty distribution of contaminants data. The geographical distribution of some toxic contaminants in Bay sediments and biota has been

characterized on a large scale. There are known "hot spots" of chemical contamination in Baltimore Harbor and the Norfolk area. However, there is not a currently available approach to gauge the impacts of individual discharges over wide areas. Similarly, it is difficult to extrapolate from watershed programs designed to reduce non-point source inputs from specific areas, to habitat benefits in higher order streams or estuaries. The environmental impacts of very diffuse sources, such as atmospheric deposition, cannot be realistically evaluated at the present time, yet it is known that these can be significant sources of toxicants (e.g., PCB). From a habitat quality perspective, monitoring of contaminants and toxicity in the environment should be designed so that linkages can be made between source reductions and improvements in the larger, integrated system.

SUMMARY OF TOXICITY INFORMATION

The Chesapeake Bay Program recently adopted a primary and secondary list of "Toxics of Concern" for the Bay.¹ These substances were selected based upon the magnitude of their use in the region, measured environmental concentrations, and their toxicity to humans, Bay species, or surrogate species. It is instructive to examine the extent of knowledge concerning the toxic effects of those chemicals on the target species included in this volume (Tables 1 and 2). These data were derived from U.S. Environmental Protection Agency Water Quality Criteria,^{15,16,17,18,19,20,21,22,23} U.S. Fish and Wildlife Service Contaminant Hazard Reviews,^{24,25,26,27,28,29,30,31,32,33,34,35} the Chesapeake Bay Program's Criteria and Standards Workgroup Data Review,¹ several water quality synthesis reviews,^{4,5,6,7,8,9,10,11,12,13} and the fish and shellfish chapters in this volume. Each of the data sources was developed through extensive literature reviews.

The data summaries in Tables 1 and 2 are useful only for illustrative and comparative purposes and are not intended to represent critical concentrations or starting points for development of water quality criteria. The separate species chapters in this volume should be consulted for more detailed information. The individual values are the geometric means of toxicity data reported for each species-chemical pair. Some values are the product of several data points and some represent single values. Data were combined across a variety of test conditions and life stages - not an appropriate procedure for strict scientific comparisons. For example, some acute values are lower than their corresponding chronic or subacute values. This is because of differences in experimental objectives between experiments from which the data were derived. If we included only those data points which were comparable between life stage, salinity, endpoints, etc., the Tables would be virtually blank.

The most important conclusion to be drawn from these summaries is that we have very little systematic knowledge about the direct effects of critical toxicants on most of the species that we consider to be important. Moreover, most of the target species are relatively high in the food chain. Neither the myriad of species which form the food chain upon which those species depend for their survival, nor the ecological keystone species usually are included in lists of "important" (or target) species. Toxicity information is biased toward easily-managed laboratory species, rather than species of recreational, commercial, and (especially) ecological importance in Chesapeake Bay.

Most of the available data are for acute toxicity. Although acute data are useful for comparison of the relative toxicity of a chemical or the relative sensitivity of a species, they are not necessarily useful for prediction of acceptable concentrations in a "healthy" environment. Chronic or sublethal data usually are considered more relevant, but are not guaranteed to define safe concentrations. The basic tradeoff is between environmental realism and specificity. The more realistic an experimentally derived datum, the less applicable it is to other situations (e.g., conditions of life stage, salinity, temperature, DO, etc.). The more generally applicable a datum (e.g., LC₅₀), the larger is the extrapolation to the real environment.

Patterns emerge from careful attention to Tables 1 and 2, and from the **Contaminants** sections of several of the chapters in this volume. Copper and mercury are universally the most toxic metals in both acute and chronic exposures. For some species, under some experimental conditions, cadmium and silver also are very toxic. Consistent with expectation, animals are more sensitive to insecticides than to herbicides (however, effects on **primary producers** caused by toxic concentrations of herbicides would present obvious dangers to consumers). Dimilin (diflubenzuron), an insecticide widely employed against gypsy moth infestations, has more severe effects on crustaceans than on mollusks, as would be expected. The antifoulant TBT is very toxic to all of the species for which data are available, but is most threatening to mollusks. We are mostly ignorant of the effects of the environmentally persistent and ubiquitous polynuclear aromatic hydrocarbons (PAH) and polychlorinated biphenyls (PCB) on species which are important either as human food or for other commercial uses, although some species are known to accumulate these compounds in Chesapeake Bay (see EASTERN OYSTER and HARD CLAM, this volume).

The available information suggests the following generalizations about relative risks to target species in Chesapeake Bay: (1) the anadromous fish (shad, herrings, striped bass, yellow perch) are very susceptible to some metals and insecticides; (2) blue crabs are more suscep-

tible to insecticides than to other contaminants; (3) molluscs (eastern oyster, hard clam, soft shell clam) are very sensitive to TBT, petroleum, and a few insecticides; (4) the best-documented bioaccumulative compounds for marine and estuarine fish are PCB and PAH.

HABITAT REQUIREMENTS FOR TOXIC SUBSTANCES

The great complexity of questions of toxicity to estuarine life, along with the lack of sufficient research on toxic effects, precludes the establishment of a complete set of critical concentrations of toxicants that will protect populations of the target species. However, some substances clearly are far more dangerous than others. Extreme toxicity, high usage, and high potential for exposure are three obvious criteria for giving special attention to some substances. A few pesticides (e.g., aldrin, TBT, toxaphene) and metals (cadmium, copper, and mercury), for example, appear to be acutely toxic to some target species at such extremely low concentrations that any exposures, especially of sensitive life stages, should be cause for concern. Chemicals which are released into the environment intentionally in large amounts (e.g., atrazine, metolachlor) and chemicals which persist for long periods of time (e.g., PCB, PAH) also pose risks to living resources.

It is impossible to establish numerical habitat requirements for the entire host of toxic contaminants that may adversely affect the target species of fish and shellfish in Chesapeake Bay. It is equally impossible to evaluate even a portion of the possible interactions that could result. It is not clear, in any case, how such numerical limits would be used; a monitoring program that would be effective in detecting toxic concentrations of a large number of contaminants in water and sediment, in all of the habitats of concern, would be logistically and economically infeasible. Only a strategy designed to minimize or eliminate inputs of toxic substances can, in the long run, be effective in protecting living resources. In the shorter term, a system of realistic assessment methods (in terms of environmental relevance and practical application) should be used to: (1) identify impacted areas; and (2) monitor progress in preventing harm from toxic contaminants to Chesapeake Bay fish and shellfish.

CONCLUSIONS

Chesapeake Bay fish and shellfish are exposed to a wide variety of toxic contaminants. These substances originate from industrial, municipal, agricultural, domestic, atmospheric, and natural (geologic) sources. In a few cases, contaminants have been associated closely with biological effects (lesions, mortalities), population effects (poor recruitment, population declines not explained by other factors), or human risks (unacceptable tissue concentrations in food species).

There is a substantial, but very incomplete, body of data on toxicity and exposures of target species, and a conspicuous absence of data sufficient to implicate, or acquit, contaminants as causes of widespread species declines or serious disruptions of the ecosystem. There is sufficient concern about hazards to the Bay's important species to warrant: (1) acquisition of better information through research, monitoring, and synthesis of existing data; and (2) dedicated attention to long term reductions in the quantities of toxic contaminants that enter the Bay from all anthropogenic sources.

RECOMMENDATIONS

Reduce contaminant loads to the Bay

Controls on point sources of toxic contaminants should be designed to be effective in preventing chronic and cumulative effects as well as acute toxic effects. Chronic effects are those caused by long term exposures, tissue accumulation, and latent toxicity (e.g., genetic damage). Cumulative effects result from accumulation of toxicants in the environment, and the combined effects of multiple toxicants within a habitat.

Agricultural, commercial, governmental, and domestic uses of chemical pesticides should be minimized through vigorous education and improved pest management programs.

Urban stormwater management programs should include toxicity reduction as a primary goal.

Atmospheric inputs of toxic substances to the Bay and its watershed should be reduced through improved controls on air pollution. The chief concerns are metals, organic compounds, PAH, and acid-forming substances that are by-products of burning fuels for power and transportation. Atmospheric transport and deposition of pesticides and other anthropogenic compounds are also of concern.

Groundwater, a significant source of fresh water to the Bay, must be protected from contamination by toxic substances.

The relative contributions of various contaminant sources should be estimated in order to prioritize control measures.

Improve designs, capabilities, and ecological relevance of monitoring programs

Identification of species of concern should include those organisms which are of significant ecological importance, regardless of their direct importance to human concerns.

Toxicity measurement methods should be environmentally realistic to include the impact of synergistic chemical and physical interactions in the ambient environment.

The relationships between bioassay endpoints (e.g., reproduction) and manifestations of ecological health (e.g., stock assessment) should be explored to improve the realism of environmental monitoring and to develop appropriate field assessment techniques.

Synthesize information on contaminant effects on Chesapeake Bay species

A complete synthesis of existing information on toxicity, exposure, and environmental contamination in Chesapeake Bay should be undertaken. If the exceedingly complex problem of understanding contaminant effects in Chesapeake Bay is ever to be solved, it will not be by

simply listing chemicals and the results of some toxicity tests. The questions must be asked, and addressed, at the levels of (1) the ecosystem, and (2) the general problem of anthropogenic contamination. The Basinwide Toxics Reduction Strategy² was a significant step in this direction. A comprehensive, ecological effects-oriented synthesis of contaminants information would be another significant advance.

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EFFECTS OF CONTAMINANTS ON FISH AND SHELLFISH

Table 1. Geometric means of literature values for acute toxicity of contaminants selected from the primary and secondary Chesapeake Bay Toxics of Concern List¹ to Chesapeake Bay target species of fish and shellfish. All values are LC₅₀ determinations, however, exposure times ranged from 48-240 hours. Metals included a variety of salts (e.g., Cl⁻, NO₃, SO₄, etc.). Life stages were pooled for calculating means. All concentrations are in µg/L⁻¹. No information was found for alewife, bay anchovy, blueback herring, or hickory shad for these toxicants. Toxics of Concern for which no toxicity information was available for target species included: alachlor, metolachlor, benzo(a)anthracene, benzo(a)pyrene, chrysene, fluoranthene, and naphthalene.

	American shad	Atlantic menhaden	Spot	Striped bass	White perch	Yellow perch	Blue crab	Hard clam	Soft clam	Eastern Oyster
arsenic				20,248 ^a	750 ^a					7500
cadmium			387	8.3 ^a 38 ^b	1712 ^a		1272		1672	2579
chromium VI			2700	16,370 ^a 58,000 ^b	10,300 ^a	36,300	75,784		57,000	10,300
copper		610	212	54 ^a	309			22	58	38
lead	< 10				2450			780	2700	2450
mercury			36	90 ^a	8.5			20.1	400	8
zinc	< 30		3800	322 ^a	2105			190	6328	263
aldrin			3.2	8 ^b	102		23			15
dieldrin				20			240			67
atrazine			8500							> 30,000
chlordane				12		10				8
dimilin						> 50,000	260	> 1x10 ⁶		> 130,000
fenvalerate										> 1000
permethrin										> 1000
toxaphene			1.7	5 ^a 5.8 ^b		12	180	< 250		23
tributyltin		4.5		< 2.0				0.05		1.5
PCB			0.5			240				10

^a tested in fresh water.

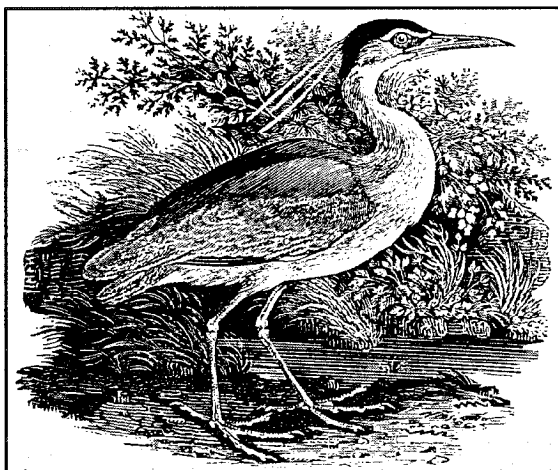
^b tested in saline water.

Table 2. Geometric means of literature values for sublethal and chronic toxicity of contaminants selected from the primary and secondary Chesapeake Bay Toxics of Concern List¹ to Chesapeake Bay target species of fish and shellfish. End points and exposure times varied. Metals included a variety of salts (e.g., Cl⁻, NO₃, SO₄, etc.). Life stages were pooled for calculating means. All concentrations are in µg/L⁻¹. No information was found for alewife, American shad, Atlantic menhaden, bay anchovy, blueback herring, yellow perch, or soft shell clam for these toxicants. Toxics of Concern for which no toxicity information was available for target species included: arsenic, alachlor, dimilin, fenvalerate, lead, metolachlor, permethrin, benzo(a)anthracene, benzo(a)pyrene, chrysene, fluoranthene, and naphthalene.

	Hickory shad	Spot	Striped bass	White perch	Blue crab	Hard clam	Eastern Oyster
cadmium		316	2		50		39
chromium VI				100	1500		
copper				50		25	50
mercury			5	10	10	14	12
zinc			430				200
aldrin		1.4				2025	0.1
dieldrin							13
atrazine							> 10,000
chlordane					353		6
toxaphene		0.03				1120	40
tributyltin	9		25			0.8	0.7
PCB		1.6					13.9

EFFECTS OF CONTAMINANTS ON BIRDS

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In the past, organochlorine pollutants such as dieldrin caused deaths of birds in Chesapeake Bay. Reproduction of birds was impaired by DDE, a metabolite of the pesticide DDT. Lead poisoning, the result of ingestion of spent lead shot used by hunters, also may have reduced survival. The banning of the most harmful organochlorine pesticides and the replacement of lead shot with steel shot have reduced mortality and reproductive problems. Other pollutants, such as cadmium, oil, and industrial chemicals may be a problem for birds in the Bay, but not enough is known about their effects to be sure. Almost certainly, the general deterioration of submerged aquatic vegetation in the bay—the result of excess nutrients, suspended sediments, and possibly herbicides—has reduced waterbird use of the Chesapeake Bay by reducing food resources.

Recommendations include: (1) developing a more complete list of contaminants in birds, (2) using field and laboratory studies to provide more information on contaminant hazards to birds, and (3) determining how much of a reduction in water turbidity, nutrients, herbicides, and other pollutants will be needed for the recovery of submerged aquatic vegetation and other foods.

INTRODUCTION

Industry, agriculture, and dense urbanization all press against the shores of Chesapeake Bay. Not surprisingly, many pollutants enter the Bay. These include agro-chemicals such as insecticides, herbicides, and fertilizers, as well as contaminants from industrial and urban sources such as oil, highway runoff, chemical reagents, and chemicals used on lawns. Municipal wastewater often carries chlorine and metals such as chromium, mercury, lead, copper, and cadmium into the Bay. Because these contaminants often bioaccumulate in the food chain, they may have direct or indirect effects on many species of birds that use the Bay, including ospreys, bald eagles, herons, waterfowl, wading birds, and shorebirds. Pollution abatement in the Chesapeake Bay represents a challenge because of the rapid population growth in the surrounding region.

BACKGROUND

By reducing survival and reproductive success, various

environmental contaminants have adversely affected populations of birds in Chesapeake Bay. The major classes of contaminants of concern are organochlorines, metals, oil, cholinesterase inhibiting pesticides, and herbicides. Organochlorines include polychlorinated biphenyls (PCBs) and pesticides such as dieldrin, kepone, and DDT and its metabolite DDE. The primary metals of concern are lead and cadmium. Both organophosphorus and carbamate pesticides, such as Abate and carbofuran, are cholinesterase inhibitors.

In this chapter we provide a general overview of effects of contaminants on birds in the Chesapeake Bay region, give detailed accounts of effects on several important species, and make recommendations for research on contaminant effects.

There is little doubt that in the past organochlorine pesticides and possibly other contaminants have killed adults and caused reproductive impairment in waterbirds in Chesapeake Bay.

Mortality

Dieldrin has been identified as a cause of death for several species of birds in the Chesapeake Bay region. Cattle egrets found dead in 1978 near Bozman in Talbot County, Maryland, and great blue herons, one from near Jamestown, Virginia, in 1970 and another from Mason Neck National Wildlife Refuge, Virginia, in 1974 were listed as cases of possible dieldrin poisoning.³¹ A series of papers that reported pesticide residues in bald eagles listed dieldrin as the likely cause of death of five bald eagles in the Chesapeake Bay.^{6,8,22,27,37,41,42} Because it is difficult to find birds killed by environmental contaminants and there is no official reporting process, it is likely that many more birds died from contaminants than were reported.

Impaired Reproduction

Organochlorine pesticides have probably had a greater effect on reproduction of birds than on adult survival. DDE was largely responsible for the decline in reproduction of bald eagles in the Bay into the 1970's. In a nationwide survey, the highest levels of most organochlorines were recorded in bald eagle eggs from the Chesapeake Bay.⁵⁵ Likewise, osprey numbers began to decline in the Bay in the 1950's and did not begin to increase until the early 1970's.^{3,20,38,39,52} Organochlorine pesticides, especially DDE, were believed responsible for population declines of ospreys in the Bay.⁵³

An estimated 15% of the barn owl population nesting in offshore duck blinds on the Maryland side of the lower Potomac River in 1972 and 1973 contained levels of organochlorines, mostly DDE and dieldrin, which may have been high enough to harm their reproduction.²³ DDE also may have impaired the reproductive success of black ducks on the East Coast in the late 1950's and into the 1960's. The more heavily contaminated areas were New York, New Jersey, and Massachusetts, but effects in Chesapeake Bay in the 1950's cannot be ruled out.²⁶ The reproduction of other species that were not studied also may have been harmed by DDE.

Other contaminants may have harmed avian reproduction in the bay but their effects may have gone unnoticed. Kepone, manufactured at Hopewell, Virginia, and dumped into the James River during production, is an example. Contamination of the tidal portion of the river was so severe that all shellfishing and finfishing was banned for several years. Kepone residues ranged from 2.4-36 mg kg⁻¹ on a wet-weight basis in the livers of great blue herons collected from Hog Island Wildlife Refuge in 1976 and 1977.²¹ Kepone was also elevated in the tissues and eggs of some bald eagles, especially those collected near the James River in the 1970's.^{44,46,55} Based on circumstantial evidence, the loss of all breeding pairs of bald eagles from the James River for a period of years might have been related in part to kepone contamination. A few osprey eggs from areas near the James River contained

elevated kepone levels.^{44,53} Unfortunately, there have been no laboratory or field studies to aid in the interpretation of these kepone residues.

Oil

Several accidents during the transport of oil have released this contaminant into Chesapeake Bay.³⁴ The birds most likely to be exposed to oil include various species of waterfowl, grebes, and loons, but a variety of other species including bald eagles and ospreys may also be exposed.^{2,35} Oiling of plumage may result in death from exposure and drowning, whereas ingestion of oil generally causes sublethal physiological effects.² An additional danger is the transfer of small amounts of oil from plumage to eggs where it may be lethal to embryos.² Lighter refined petroleum products such as No. 2 fuel oil and gasoline are far more toxic than heavier products such as bunker C. Nonpoint sources of oil pollution from boating activities and urban runoff are probably greater than point sources such as spills. Damage and disturbance of bird habitats by oil pollution may cause displacement of populations and reductions of important foods.²

EFFECTS ON KEY SPECIES

Bald Eagle

Exposure to organochlorine pesticides from agriculture and mosquito control was the primary cause for the decline of the bald eagle in Chesapeake Bay in the 1950's into the 1970's. Dieldrin caused direct mortality of adult bald eagles, and DDE profoundly reduced reproductive success. Survival and successful reproduction of bald eagles in Chesapeake Bay requires that eggs contain no more than an average of 2 ppm DDE, 0.3 ppm dieldrin, or 5 ppm PCBs on a wet-weight basis. Bald eagle eggs collected after they failed to hatch from Chesapeake Bay nests during the 1970's contained mean concentrations of about 10 ppm DDE, 1 ppm dieldrin, and 25 ppm PCBs, plus other organochlorine pesticides and their metabolites. The concentrations in eggs during 1973-79 were among the highest for any bald eagle population in the United States. DDE, dieldrin, and PCBs were the chemicals of greatest concern for reproduction.

Concentrations were significantly lower in 1980-84 (about 4.5 ppm DDE, 0.3 ppm dieldrin, and 15 ppm PCBs) than in 1973-79. During the later period, the population began to increase and reproductive success returned to normal. Elevated DDE residues (≥ 4 mg kg⁻¹) in bald eagle eggs have been most closely related to poor production of young and eggshell thinning. The presence of PCBs and other contaminants also has been associated with poor reproduction and eggshell thinning, but these associations are probably due to the fact that where DDE is high, these other chemicals are also high.^{54,55}

Tissues of bald eagles found dead in the Chesapeake Bay region have been analyzed for organochlorine pesticides and PCBs. In the early 1970's, the brains of a few eagles had lethal or highly elevated concentrations ($\geq 4 \text{ mg kg}^{-1}$) of dieldrin, but concentrations rapidly declined thereafter.^{6,8,22,27,37,42,46,47}

Metals do not seem to have been involved in the decline of bald eagles in Chesapeake Bay. Mercury residues in eggs were about one-tenth of the residues associated with reductions in reproductive success in other species.^{54,55} Four bald eagles from the greater Chesapeake Bay region are known to have died of lead poisoning, although three were found dead far from the Bay.⁴⁷ High lead concentrations in eagles ($\geq 10 \text{ mg kg}^{-1}$ wet weight) in the liver is an indication of lead poisoning) are from ingestion of lead pellets in prey (primarily waterfowl) that were killed or crippled by hunters, and not from contamination of the environment from other sources.³²

Other contaminants such as carbamate and organophosphorus pesticides have been implicated in the mortality of bald eagles in the Chesapeake Bay region.⁴⁷ However, these pesticides did not reach the eagles through the aquatic food chain but from consumption of illegal poisoned baits or terrestrial animals that had acquired these pesticides from illegal baits or pesticide use in normal agricultural practice. Excessive mortality from these chemicals may have slowed recovery of the population. Restrictions on the use of some chemicals, such as carbofuran, may prove beneficial to bald eagles and other species.

Osprey

Reproductive success of the osprey population in Chesapeake Bay was reduced by the adverse effects of organochlorine pesticides, primarily DDE. However, the harm was generally far less serious to ospreys than to bald eagles. Direct mortality from agricultural chemicals was not detected.

Osprey eggs from several areas around the Bay in the 1960's and 1970's contained about 3 mg kg^{-1} DDE, $3\text{--}10 \text{ mg kg}^{-1}$ PCBs, and several other organochlorine pesticides at lower concentrations.^{53,58} Eggshell thinning in some samples approached levels ($> 15\%$) that have been associated with egg breakage and subsequent poor reproduction and population declines.^{4,24,53} Among the contaminants in osprey eggs, DDE has been most closely associated with eggshell thinning and was apparently responsible for impaired reproduction.⁵³ Although in eggs concentrations of PCBs generally exceeded those of DDE, PCBs were not associated with adverse effects on shell thickness and production of young. Trends in organochlorine concentrations in eggs have been variable, but levels in general have been stable or declining.⁵³ During the 1970's and early 1980's concentrations of or-

ganochlorine pesticides generally declined in tissues of dead ospreys in the Bay during the 1970's and early 1980's, but PCB concentrations remained unchanged.⁵⁷

Various elements, including chromium, copper, zinc, arsenic, cadmium, mercury, and lead, do not seem to have had an adverse effect on ospreys in Chesapeake Bay. Concentrations in tissues of birds found dead around the bay were generally normal.^{56,57} Although few data are available on the synergistic effects among different elements, we believe that harmful synergistic effects on birds are unlikely at the levels of these elements in the Bay.

Canvasback

Although our knowledge of the effects of various contaminants, especially metals, on canvasbacks is incomplete, there is no evidence to date that canvasbacks have suffered direct toxic effects from any environmental contaminants in the Chesapeake Bay, although indirect effects through depletion of submerged aquatic vegetation may have occurred.

Except for seaducks, canvasbacks had the highest levels of cadmium in liver and among the highest of all ducks in kidney. Lead, in contrast, was not especially high in canvasbacks compared with dabbling ducks and seaducks. Zinc and copper concentrations were not especially different in canvasbacks than in other ducks and were not considered harmful.¹¹ Cadmium concentrations in canvasbacks were generally below concentrations found in a laboratory study on mallards to be associated with lesions in kidneys.⁴⁹ However, a small percentage of canvasback livers had greater than 7 mg kg^{-1} cadmium, a level associated with changes in energy metabolism in mallards.¹⁰ Lead in foods might be a greater source of lead for canvasbacks than lead shot.¹¹ From a study of lead levels in blood and a blood enzyme assay to estimate exposure of canvasbacks in Chesapeake Bay to lead, Dieter⁹ concluded that foods were more of a cause of elevated lead than the ingestion of lead shot. The recent switch in the diet of canvasbacks from submerged aquatic vegetation to clams was not believed to increase exposure to lead or cadmium. In fact, the levels of both metals were generally higher in plants than in clams.¹²

Organochlorine pesticide and PCB levels in canvasbacks in Chesapeake Bay in 1973 and 1975 were believed to be in a safe range when compared with levels known to harm survival and reproduction.⁵¹

Organochlorine and mercury levels in canvasback eggs from the prairie pothole region of the United States and Canada in 1972 and 1973 were generally below concentrations believed to affect reproduction.⁴⁵ Although canvasbacks do not nest in Chesapeake Bay, mercury and many organochlorines are eliminated slowly from the body, and, therefore, levels of these substances in eggs

would reflect exposure not only on the breeding ground but on the wintering ground as well.

Physiological and other sublethal effects of contaminants could indirectly alter survival or reproduction in canvasbacks. For example, lighter-weight canvasbacks on Chesapeake Bay were shown to have lower overwinter and annual survival probabilities.¹⁶ However, the most likely reason canvasbacks might be underweight is not a toxic effect of contaminants on the birds but reductions in the abundance of submerged aquatic vegetation in the Bay, and even this more likely connection has not been proven. Reductions in aquatic plants are probably due to contaminants as well, but such effects on the health of canvasbacks would be indirect. The question of whether cadmium is altering the energy metabolism of a small percentage of canvasbacks remains unanswered.

American Black Duck

Apart from lead shot poisoning, which should decrease with the replacement of lead shot with steel shot, contaminants do not seem to be a threat to black ducks in Chesapeake Bay. This conclusion is tempered by the lack of a complete inventory of contaminants and their effects on waterfowl in the Bay.

Lead concentrations generally have been higher in black ducks and other dabbling ducks than in seaducks and diving ducks, a fact attributable to the higher densities of spent shot in areas inhabited by dabbling ducks. In contrast to canvasbacks, accumulation of lead through the food chain was not considered as large a source as lead shot for black ducks. Cadmium, zinc, and copper in black ducks were below levels believed to be harmful to birds.¹¹

Measurements of organochlorines in black ducks from Chesapeake Bay date back to a survey of eggs in 1964.⁴⁰ Compared with DDE levels in eggs of black ducks from states such as New York, New Jersey, and Massachusetts, eggs of black ducks from Chesapeake Bay were fairly clean. Coupled with the results of subsequent surveys in 1971 and 1978, these findings indicate that organochlorine pesticides or PCBs probably did not pose a hazard to black ducks, at least not since the egg surveys began, and these chemicals are even less likely to be a problem today.^{17,25,40}

Black ducks in Chesapeake Bay were also part of the duck wing monitoring program for pesticides and PCBs that was started in 1965 and lasted into the 1980's. Because pools of wings from Maryland and Virginia were analyzed, origins of specific wings could not be identified, but it is reasonable to assume that many came from Chesapeake Bay. As with the black duck egg surveys, the wing surveys showed that black ducks from the Chesapeake Bay area contained lower levels of most organochlorine pesticides and PCBs than black ducks from states such as Massachusetts, New York, and New Jersey. Moreover, or-

ganochlorine pesticides and PCBs have steadily declined in black duck wings from the Chesapeake Bay area.^{7,18,19,36,48,50}

Wood Duck

Information on concentrations and effects of environmental contaminants on wood ducks in Chesapeake Bay is scarce. However, much of the information listed in the sections on other ducks is applicable to some extent to wood ducks.

Concentrations of several metals were measured in wintering wood ducks collected primarily from fresh water marshes bordering tributaries of rivers entering Chesapeake Bay. Concentrations of metals were lower than or about equal to levels in other ducks from the Bay, except for lead, which was higher in wood ducks. Lead was the only metal in wood ducks considered high enough to be associated with sublethal effects, such as physiological changes. For wood ducks and other species of dabbling ducks (mallards, black ducks, and pintails), ingestion of lead shot was considered the probable cause of elevated lead in liver. Lead through the food chain was not considered to pose a significant hazard.^{11,43}

Redhead

We found no publications describing contaminant levels in redheads from Chesapeake Bay, but the information presented for other diving ducks is generally applicable to this species.

Wading Birds

There is too little information on contaminant levels and effects in wading birds in Chesapeake Bay to make a clear assessment of possible adverse effects. A survey of PCBs and organochlorine pesticides in the brains and carcasses of wading birds found dead in Chesapeake Bay and its tributaries was conducted in the late 1960's and 1970's. Except for two great blue herons in which dieldrin levels in the brain were in a potentially dangerous range, concentrations of PCBs and pesticides in several great blue herons, green-backed herons, and snowy egrets were too low to have been the cause of death. Two cattle egrets were reported to have died of dieldrin poisoning.³¹ In the early 1970's, residues of PCBs and organochlorine pesticides in the eggs of green-backed herons and cattle egrets from the Potomac River were below levels believed to affect reproduction.³⁰

RECOMMENDATIONS

Apart from isolated examples of possible continuing effects of contaminants on individual species of birds, there is little evidence suggesting that contaminants in Chesapeake Bay are currently posing a serious hazard to birds from direct toxicity. Nevertheless, monitoring of contaminants in waterbirds should continue, especially in the

most contaminated areas of the Bay. The direct effects of these contaminants on birds is probably less important than the indirect effects on habitat by excess nutrients, suspended sediments, and possibly herbicides. The loss of submerged aquatic vegetation in the Bay is perhaps the best example of an indirect effect of pollutants on waterfowl abundance and distribution.

Others have come to much the same conclusion. In a review of organochlorine pollutants and birds in Chesapeake Bay, Ohlendorf²⁸ advised, "In the Chesapeake Bay attention should be focused on fish-eating birds, primarily bald eagles and ospreys, but it is unlikely that organochlorines will represent a serious threat to these species, or others of the Chesapeake Bay region". In another review paper dealing with continuing organochlorine pesticide and PCB problems in the 1980's, Fleming *et al.*¹⁴ listed many potential problems across the United States, but none in the Chesapeake Bay.

Perry³³ concluded, "Although some of the studies of pollutants in Chesapeake Bay waterfowl have shown some cause for concern, in general, pollutants in tissue and eggs of waterfowl are below levels normally considered to cause adverse effects. Monitoring of contaminants in waterfowl should continue, especially in the most contaminated areas of the Bay, but the direct impact of these pollutants on birds is probably less important than the indirect effects on waterfowl habitat from pollutants such as nutrients, suspended sediments, and perhaps herbicides".

In the most recent review of contaminant effects on birds in Chesapeake Bay, Ohlendorf and Fleming²⁹ stated, "In the Chesapeake Bay high levels of cadmium and lead in seaducks, lead in dabbling ducks, and DDE in some ospreys and bald eagles are the current avian contaminant issues".

Needed Research on Direct Effects on Species

Two kinds of research on direct effects are needed: additional field sampling to arrive at a more complete list of contaminants and research on the effects of certain already known contaminants, such as lead and cadmium, on the health and reproductive success of birds.

Contaminants such as selenium have not been adequately assessed in birds or their eggs. Possible sources of selenium in Chesapeake Bay, such as coal-fired electrical generating plants and selenium from bay sediments, deserve study. The documented severe effects of selenium on survival and reproduction of birds in California and its discovery at elevated levels in San Francisco Bay suggest that this element should be measured in at least a few species from Chesapeake Bay. Selenium was found at high levels in fish from the James River near the Chester-

field coal-fired power plant, an area frequently used by ospreys, bald eagles, and many herons and egrets (personal communication: Dan Audet).

Other elements and organic compounds, especially when already known to occur at elevated levels in plants or animals eaten by birds, should be measured in representative birds. When new contaminants are discovered at elevated levels and information does not already exist on their toxicity to birds, laboratory and field research should be initiated. In some cases, laboratory tests may suffice to determine tissue and egg residues associated with effects on health, survival, and reproduction. When residues seem to be in a dangerous range, field research should be conducted to relate residues to the reproductive success of species that nest in the Bay.

With the replacement of lead shot with steel shot, lead poisoning in puddle ducks should decrease soon. But the significance of lead derived through the food chain by canvasbacks and seaducks needs continued study. The effects of high cadmium residues in seaducks are unknown; research is needed to determine potential effects on health and reproduction.

Abate is an organophosphorus pesticide used as a mosquito larvicide in marshes bordering the Bay. Although it has a short half-life and a comparatively low toxicity to birds, it caused a surprising degree of reproductive impairment when fed to breeding adult mallards and their young at 1 ppm on a dry-weight basis in a laboratory study.¹⁵ There appears to be an unidentified detrimental effect of Abate on ducklings or on maternal behavior. Additional field and laboratory research is needed to confirm the results of the original reproductive study and to determine why the ducklings died.

An expanding colony of black-crowned night herons nests in the Patapsco River estuary of the heavily contaminated Baltimore Harbor.¹³ These herons feed in some of the most industrialized parts of the harbor. If a fish-eating species of bird were to be affected by contaminants somewhere in Chesapeake Bay, it might be these herons. Contaminants and their effects on these herons need to be identified. Considerable nationwide research has already been conducted to determine how the black-crowned night heron can be used in a monitoring program to measure contaminant levels and effects in estuaries. Research on this colony in Chesapeake Bay may fit into this program.

Another potential area of research relates to the construction of storm water retention ponds and other wetlands in urban areas. These manmade wetlands are used to prevent sediments and chemical pollutants from reaching Chesapeake Bay and other estuaries.¹ When properly designed, these wetlands attract many kinds of birds. The

benefits of a reduction in contaminants entering Chesapeake Bay may be offset by an increase in contaminants in many of these small, urban wetlands.

Needed Research on Indirect Effects on Food

Indirect toxic effects are defined as those that limit the availability of food or cover for birds. In Chesapeake Bay, effects on foods are probably more important than effects on cover and could indirectly affect the health, survival, or reproduction of birds. Indirect effects may prove more harmful than direct toxic effects on birds in Chesapeake Bay

The reduction in submerged aquatic vegetation in parts of Chesapeake Bay is potentially the most important pollution-induced change in foods for birds such as waterfowl. Although the canvasback has adapted to a loss of submerged aquatic vegetation by switching its diet from vegetation to mollusks, the consequences of this switch are not fully known.³³ For other species such as the redhead duck which is less capable of switching its diet, the loss of submerged aquatic plants has no doubt resulted in great reductions in the winter carrying capacity of the Bay. The same problems might be expected for fish-eating birds or birds relying on invertebrates in areas where these foods have been affected by pollution; however, in most cases, these relationships have not been demonstrated.

When the abundance and distribution of food changes because of pollutants, the abundance and distribution of birds should change in response. However, the research needed to demonstrate this connection and what actions are required for foods to recover is difficult to conduct. Part of the difficulty is that many birds that winter in Chesapeake Bay breed elsewhere where other problems, such as the effect of drought on waterfowl, may also influence bird abundance. Even if most of a species' problems were caused by pollution of Chesapeake Bay, it would be difficult to design research with proper control areas and with populations resident long enough in control or polluted areas to make good comparisons. Nevertheless, various kinds of innovative research should be started to show the connection between pollutant-induced changes in food abundance and effects on birds.

Among the kinds of innovative research needed are studies that show how much of a reduction in water turbidity, nutrient loading, herbicide runoff, and other contaminant effects on food bases is needed for foods to recover. Also, when foods recover, will bird numbers increase in that area or will other factors, some removed from Chesapeake Bay, keep bird numbers where they are?

Much more needs to be learned about how the health of birds may be affected by shortages and changes in kinds

of foods. For example, is the health and survival of wintering waterfowl affected by a change from the traditional diet or by less available food? Is reproductive success impaired by poor winter nutrition? Do dietary shortages make birds more susceptible to hunting, disease, or predation? Are birds that traditionally wintered in Chesapeake Bay shifting their wintering grounds elsewhere?

In addition, it is unknown how food items and birds will change in response to clean-up efforts in the Bay. If contaminated sediments are preventing invertebrates or plants from living in certain areas, how quickly will these foods return if sediments are removed or covered by clean sediments? How quickly will the birds return? Some research is needed in which sediments in at least small areas are restored to a clean state and the recovery of plant and animal life followed.

The same is true of research on water quality. Can an experiment be conducted in which water quality in at least a small area is improved to see how quickly plant and animal life recovers? Such research might include the use of exclosures to keep suspended sediments out, as well as means to filter and purify incoming water. Research could also include the seeding of cleaned areas with plants and invertebrates to compare recovery rates to those in unseeded areas.

At the very least, plant and animal recoveries (and bird use) should be followed in areas that naturally recover as pollution control in the Bay proceeds. Ideally, a coordinated laboratory and field research effort on indirect contaminant effects on birds should be initiated as soon as possible to guide recovery efforts.

CONCLUSION

Although organochlorine pesticides, and perhaps PCBs, affected birds in Chesapeake Bay in the past, there is little evidence indicating they are still causing great harm. Certain metals, such as lead and cadmium, may be a problem for canvasbacks and other ducks, but more research on effects is needed. A search for other contaminants, such as selenium and industrial pollutants, is warranted in birds. The most harmful contaminant effects may be indirect ones on food supplies, such as the reduction in submerged aquatic vegetation caused largely by water turbidity. Research on contaminant effects on avian foods should guide and accompany recovery efforts on Chesapeake Bay.

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GLOSSARY

Acanthocephalan - any of the invertebrate phylum Acanthocephala, a group of small parasitic wormlike acelomates.

Acetylcholinesterase - a membrane-bound enzyme which plays an important role in the transmission of nerve impulses.

Acidic - hydrogen containing molecules or ions able to give up a proton (H^+) to a base; having a pH less than 7; compare basic and pH.

Alimentary - the tubular passage from the mouth to the anus, which functions in digestion, absorption, and elimination of unabsorbed nutrients.

Alkaline - a hydroxide which when dissolved in water forms a basic solution containing hydroxide ions (OH^-); having a pH greater than 7.

Ambient - an encompassing atmosphere; characterizing the surrounding environment.

Ammonia - (NH_3) a nitrogenous waste product of cellular metabolism; an alkaline compound which is highly soluble in water forming ammonium ions (NH_4^+); toxic in high concentrations.

Amphipod - a small crustacean of the phylum Arthropoda, with a laterally compressed body and sessile eyes, if present. Most species are marine although some freshwater, terrestrial, and parasitic forms exist.

Anadromous - pertaining to fishes that move from their primary habitats in the oceans to freshwater rivers and streams to spawn; compare catadromous.

Anhydrase - enzyme involved in securing oxygen and carbon dioxide from the blood to be used in respiration.

Anoxia - the absence of oxygen; in aquatic systems, the lack of dissolved oxygen available to organisms for aerobic respiration, generally $< 0.5 \text{ mgL}^{-1}$; compare hypoxia.

Basic - having a pH greater than 7; compare alkaline.

Basophil - a type of white blood cell characterized by the coarse granules it contains; has an important role in fighting infection.

Benthos - collectively, all organisms living in, on, or near the bottom substrate in aquatic habitats. (adj. benthic)

Bioaccumulation - within an organism, the increase over time in the concentration of substances not easily excreted or metabolized, e.g. pesticides and heavy metals, acquired principally through foods eaten.

Blastula - the stage of embryonic development characterized by a hollow ball of cells with walls only one cell layer thick, produced as a result of the cleavage of an ovum.

BOD (Biological Oxygen Demand) - a measurement of the amount of oxygen needed by aerobic biological processes that break down organic matter in water.

Brood - to hatch; to produce by incubation; a set of offspring produced at the same birth or from the same set of eggs.

Browser - a terrestrial animal that eats twigs or shoots, with or without attached leaves.

Calanoid - a free-living, largely planktonic copepod of the order Calanoida.

Calorie - the quantity of heat necessary to raise the temperature of one gram of pure water one degree Celsius; a unit measure of energy value of food.

Catadromous - pertaining to fishes that move from their primary habitats in fresh water to the oceans to spawn, e.g. eels.

Catalase - an enzyme present in cells which catalyzes the decomposition of hydrogen peroxide (H_2O_2) to molecular oxygen (O_2) and water (H_2O).

Caudal - pertaining to the tail.

Chironomid - an insect of the family Chironomidae of the order Diptera (the flies). Larvae of most species are aquatic, adults are soft-bodied and winged; known as the midges.

Cladoceran - any of the group of small crustaceans of the class Brachiopoda. Known as water fleas, almost all species inhabit freshwater; often represented by the genus *Daphnia*.

Clutch - the aggregate of the eggs or young of birds

Coleopteran - any of the insect order Coleoptera, the beetles.

Compensation Depth - the depth at which the amount of oxygen a plant produces through photosynthesis equals the amount of oxygen needed for respiration. Below this depth a photosynthetic cell cannot survive because there is not enough light for it to produce as much energy as it requires for its own respiration.

Coniferous - cone-bearing vascular plant.

Copepod - a sub-class of the class Crustacea. Most are planktonic where they form an important food for higher trophic levels such as fish. Some are parasitic.

Cultch - hard substrate for larval "spat" oysters to attach to and mature; often other oyster shells.

Cyclopoid - a copepod belonging to the class Cyclopoida, includes benthic and planktonic members living in both fresh and salt water. Many are parasitic.

Deciduous - perennial plants that shed leaves before winter cold.

Dehydrogenase - an enzyme which catalyzes the oxidation of a certain substance, causing it to give up hydrogen.

Demersal - living on or near the bottom of a body of water; mid-water and bottom-living fish as opposed to surface fish and shellfish.

Detritus - loose organic material formed from decomposing organisms, a primary food source for some organisms.

Diatoms - a unicellular form of algae in the class Bacillariophyceae of the division Chrysophyta. They are golden-brown in color, with silicon dioxide cell walls. Common benthic and planktonic forms in marine and freshwater systems. Important primary producers, providing a potential food source to higher trophic levels.

Dioecious - male and female sexes manifested in separate individuals; compare monoecious.

Dissolved Oxygen (DO) - free oxygen available to organisms and chemical processes in an aquatic environment; expressed as milligrams per liter (mgL^{-1}), parts per million (ppm), or percent saturation (%).

Dorsal - belonging to or situated near the back of an animal or one of its parts. Compare ventral.

EC₅₀ (Median Effective Concentration) - the concentration of a substance in an environment which produces sub-lethal responses in fifty percent of a specified population of test organisms.

Entrainment - to draw in and transport by the flow of a fluid.

Eutrophication - the process by which a body of water becomes rich in dissolved nutrients, often leading to excessive algal growth, increased metabolism, low dissolved oxygen and changes in community composition.

Extruded - pushed out by force.

Fecundity - the number of young produced by a species or individual.

Fingerling - a young fish, from two weeks after the absorption of the yolk sac to one year of age.

Fledgling - a young bird capable of leaving the nest and surviving.

Gametogenesis - the process of forming gametes such as egg and sperm.

Gastrulation - the stage of development in which the single cell layered blastula becomes a three cell layered embryo; compare blastula.

Genotype - the sum total of genetic information within an organism, regardless of its appearance or phenotype.

Grazer - an organism which feeds on growing herbage, attached algae, or phytoplankton; herbivore.

Guano - the excrement of seafowl, high in phosphorus and nitrogen.

Hardness - the condition of water characterized by the presence of dissolved calcium or magnesium salts, expressed in mgL^{-1} .

Hematocrit - an instrument for determining the relative amounts of plasma and corpuscles in blood.

Histology - the science of the detailed structure of plant and animal tissues and organs.

Hydrocarbons - a general term for organic compounds containing only hydrogen and carbon.

Hydrology - the study of water, including rain, snow, and water on and within the earth's surface, concerning its properties, distribution and utilization.

Hymenopteran - any insect of the order Hymenoptera, including wasps, bees, and ants.

Hypereutrophy - the condition of a body of water having excess nutrients; compare eutrophication.

Hypoxia - the condition of low dissolved oxygen in aquatic systems, typically with a concentration $< 2 \text{ mgL}^{-1}$ but $> 0.5 \text{ mgL}^{-1}$.

Impingement - refers to fish being trapped against screens in the gates of a dam or power plant intake by rushing water.

Interspecific - refers to relations or conditions between different species.

Intraspecific - refers to relations or conditions between individuals within the same species.

Isopod - a small crustacean of the phylum Arthropoda, usually dorso-ventrally flattened, with sessile eyes; they show a great variety of form, size and habit. Most are marine, but some are freshwater or terrestrial; also, some isopods are parasitic.

Juvenile - a physiologically or sexually immature individual.

Juvenile Index - an estimate of the size of a juvenile population.

kcal (Kilocalorie) - one-thousand calories; compare calorie.

LC₅₀ (Median Lethal Concentration) - the concentration of a substance necessary in an environment to produce death among fifty percent of a specified population of test organisms.

LD₅₀ (Median Lethal Dose) - the amount of a substance necessary in an environment to produce death among fifty percent of a specified population of test organisms.

Limnetic Zone - the area between the surface and compensation depth; the lighted zone of the water column.

Littoral Zone - the area between high and low water; the intertidal zone.

Mallophaga - a suborder of insects containing biting lice, usually skin parasites of birds.

Megalopa - the last larval stage of crabs which settles to the bottom and metamorphoses into a juvenile.

Meristic - segmented; divided into parts.

Mesohaline - the region of moderately saline water, generally eight to fifteen parts per thousand.

Monoecious - having male and female sex organs in one organism; hermaphroditic.

Monomeric - derived from one part.

Monomorphic - an organism developing with no or very little changes during its life history.

Moribund - in the process of dying; a state of suspended activity or growth.

Morphology - the study of form and structure of organisms as opposed to their function.

Morphometry - the study of the structural measurements of a lake and its basin.

mtDNA - mitochondrial deoxyribonucleic acid; DNA found in the cellular organelle called the mitochondria.

Myotome - a muscular segment of primitive vertebrates and segmented invertebrates.

Nauplii - the free-swimming, first larval stage of copepods.

Nekton - pelagic animals capable of swimming with a directed velocity as opposed to plankton.

Nematode - a worm in the class Nematoda of the phylum Aschelminths, small unsegmented with an elongated body, pointed at both ends, found in terrestrial, fresh water, and marine systems. Most species are free-living in aquatic sediments and in soil. Parasitic species comprise one of the most important parasitic animal groups.

Neutrophil - a white blood corpuscle whose granules stain only with neutral stains.

Nitrate - an anion form of nitrogen and oxygen (NO_3^-), generally the primary inorganic form of nitrogen in aquatic systems which is readily available to plants as a nutrient.

Oligohaline - the region of low salinity water, generally with salinity of 0.5 to 5.0 parts per thousand.

Ontogenetic - relating to the history of growth and development of an individual.

Organochlorine - any of the group of chlorinated hydrocarbon pesticides, such as DDT and dieldrin.

Otolith - a calcareous concretion in the internal ear of a vertebrate.

Pectoral - in or about the chest region of vertebrates.

Pelagic - pertaining to open waters or the organisms which inhabit these waters; the region of the open sea extending from the surface to the depth of light penetration; compare littoral.

Perivitelline - pertaining to the substance or area surrounding the yolk of an egg.

pH - a logarithmic index of hydrogen ion (H^+) concentration in water, expressed within a range of 0 to 14, where values less than 7 are considered acidic and values greater than 7 are considered alkaline; the value 7 is neutral.

Phenotype - the physical appearance of an organism resulting from the interaction of its genetic constitution and environmental influences.

Phytoplankton - the free-floating or weakly motile group of aquatic unicellular plants; the photosynthetic members of plankton.

Piscivorous - preying upon fish; fish-eating.

Plankton - those organisms free-floating or drifting in open water having their movements determined by the motion of the water; extremely important food source for many animals.

Pochard - any of the diving ducks of the genus *Aythya*, with large heads and feet, and legs placed far back on their body.

Polychaete - a class of Annelida; chiefly marine worms characterized by a cylindrical body form, paired appendages, and segmentation. Both mobile (errant) and sessile forms exist. In marine systems they are mostly benthic, living in the sediment or substrate.

Polyhaline - the region of high salinity water, generally with salinity of eighteen to thirty parts per thousand.

Primary Production - the mass of plant material produced per unit area.

Pterygiophore - a cartilaginous ray in the fin of a fish.

Rheotactic - refers to movement against a current.

Riparian - relating to the bank or shoreline of a body of water.

Rotifer - a small aquatic animal of the phylum Rotifera with circles of cilia at the anterior end. The majority of species inhabit fresh water.

Salinity - the amount of dissolved salts in water, primarily sodium chloride (NaCl). Expressed as the number of grams per 1000 grams of water, but generally as parts per thousand (ppt).

Siltation - the deposition or accumulation of silt.

Silviculture - an area of forestry which deals with establishment, development, reproduction and management of forest trees.

Softness - a condition of water characterized by the absence of dissolved calcium and magnesium salts.

Substrate - surface or medium in or on which an organism lives.

Synergistic - the quality of two or more distinct agents to interact such that the total effect is greater than the sum of the individual effects.

Teleost - any member of a group of fish with bony rather than cartilaginous skeletons which includes almost all fish.

Thrombocyte - in non-mammalian vertebrates, spindle shaped cells involved in blood clotting.

Trematode - any of the class Trematoda of the Phylum Platyhelminthes (the flatworms), all members are parasitic, commonly referred to as flukes.

Tricopteran - any of the insect order Tricoptera, commonly called caddisflies; their larvae are aquatic.

Trochophore - the free-swimming pelagic larval form of many annelids and some mollusks.

Trophic Level - broad class of an ecosystem in which all organisms procure food in the same general manner. The first trophic level is green plants, the second level is herbivores, and the third level is the carnivores that eat the herbivores.

Turbidity - a measure of water opaqueness measured as suspended solids per liter of water (mgL^{-1} TSS) or Secchi disc depth (in meters [m])

Veliger - the second pelagic larval stage of some mollusks.

Ventral - belonging to or situated near or on the anterior or lower surface of an animal that is, opposite the back.

Viscera - the organs contained within a body cavity.

Year Class - a group of animals born during a particular year, primarily used for fish.

Young of Year - an animal born in the present year.

Zoea - an early planktonic larval stage of crabs and shrimp.

Zooplankton - the group of floating or weakly swimming animals transported by water motion; abundant food source for many aquatic species.

COMMON AND SCIENTIFIC NAMES OF ORGANISMS MENTIONED IN THIS REPORT

PLANTS

ALGAE

Hollow green seaweed	<i>Enteromorpha</i> spp.	Sea lettuce	<i>Ulva lactuca</i>
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SUBMERGED AQUATIC VEGETATION

Eelgrass	<i>Zostera marina</i>	Ribbonleaf pondweed	<i>Potamogeton epihydrus</i>
Grassleaf pondweed	<i>Potamogeton pusillus</i>	Sago pondweed	<i>Potamogeton pectinatus</i>
Horned pondweed	<i>Zannichellia palustris</i>	Shoal grass	<i>Halodule beaudettei</i>
Muskgrass	<i>Chara</i> spp.	Southern naiad	<i>Najas guadalupensis</i>
Naiad	<i>Najas</i> spp.	Water milfoil	<i>Myriophyllum</i> spp.
Nuttall waterweed	<i>Elodea nuttallii</i>	Waterweed	<i>Elodea canadensis</i>
Pondweed	<i>Potamogeton</i> spp.	Widgeon grass	<i>Ruppia maritima</i>
Redhead grass	<i>Potamogeton perfoliatus</i>	Wild celery	<i>Vallisneria americana</i>

EMERGENT PLANTS

Arrow-arum	<i>Peltandra virginica</i>	Giant burreed	<i>Sparganium eurycarpum</i>
Arrowleaf tearthumb	<i>Polygonum sagittatum</i>	Halberdleaf tearthumb	<i>Polygonum arifolium</i>
Bulrush	<i>Scirpus</i> spp.	Needle rush	<i>Juncus roemerianus</i>
Bulrush, hardstem	<i>Scirpus acutus</i>	Pickerelweed	<i>Pontederia cordata</i>
Bulrush, olney	<i>Scirpus olneyi</i>	Saltmarsh cordgrass	<i>Spartina alterniflora</i>
Bulrush, river	<i>Scirpus fluviatilis</i>	Saltmeadow hay	<i>Spartina patens</i>
Burreed	<i>Sparganium</i> spp.	Sedges	<i>Carex</i> spp.
Buttonbush	<i>Cephalanthus occidentalis</i>	Spatardock	<i>Nuphar advena</i>
Common reed	<i>Phragmites communis</i>	Stiff arrowhead	<i>Sagittaria rigida</i>
Common three-square	<i>Scirpus americanus</i>	Smartweeds	<i>Polygonum</i> spp.
Cordgrass	<i>Spartina</i> spp.	Twigrush	<i>Cladium mariscoides</i>
Cattail	<i>Typha</i> spp.	Waterlily	<i>Nymphaea</i> spp.
Delta duck potato	<i>Sagittaria platyphylla</i>	Waterlily, banana	<i>Nymphaea mexicana</i>
Dotted smartweed	<i>Polygonum punctatum</i>	Wild rice	<i>Zizania aquatica</i>
Duckweeds	<i>Lemna</i> spp.		

SHRUBS

Swamp privet	<i>Forestiera acuminata</i>	Hightide bush	<i>Iva frutescens</i>
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TREES

Ash	<i>Fraxinus</i> spp.	Hornbeam	<i>Ostrya virginiana</i>
Bald Cypress	<i>Taxodium distichum</i>	Ironwood	<i>Carpinus caroliniana</i>
Beech	<i>Fagus grandifolia</i>	Maple, red	<i>Acer rubrum</i>
Bitternut	<i>Carya cordiformis</i>	Maple, silver	<i>Acer saccharinum</i>
Cherry, black	<i>Prunus serotina</i>	North American tuliptree	<i>Liriodendron tulipifera</i>
Elm, American	<i>Ulmus americana</i>	Oak	<i>Quercus</i> spp.
Gum, black	<i>Nyssa sylvatica</i>	Oak, chestnut	<i>Quercus prinus</i>
Gum, sweet	<i>Liquidambar styraciflua</i>	Oak, northern red	<i>Quercus rubra</i>
Hickory, water	<i>Carya aquatica</i>	Oak, Nuttall's	<i>Quercus nuttallii</i>

Oak, pin
Oak, southern red
Oak, swamp white
Oak, water
Oak, white
Oak, willow

Quercus palustris
Quercus falcata
Quercus bicolor
Quercus nigra
Quercus alba
Quercus phellos

Pine, loblolly
Pine, shortleaf
Pine, Virginia
Sycamore
Willow

Pinus taeda
Pinus echinata
Pinus virginica
Platanus occidentalis
Salix spp.

OTHER PLANTS

Corn
Honeysuckle
Poison ivy
Sorghum

Zea mays
Lonicera japonica
Toxicodendron radicans
Sorghum vulgare

Soybean
Wheat
Whitetop grass

Glycine max
Triticum spp.
Fluminia festucacea

ANIMALS

INVERTEBRATES

Ark clam
Baltic clam
Barnacle
Black-fingered mud crab
Blue crab
Blue mussel
Brackish water clam
Brine shrimp
Burrowing anemone
Burrowing mayfly
Caddisfly
Caddisfly
Calanoid copepod
Calanoid copepod
Carnivorous flatworm
Channeled whelk
Ciliate protozoan
Colonial hydroid
Colonial hydroid
Comb jelly
Commensal nemertean worm
Coot clam
Crab nemertean
Cyclopoid copepod
Cyclopoid copepod
Cyclopoid copepod
Cyclopoid copepod
Eastern oyster
Ectoparasitic snail
Equal-clawed mud crab
Fairy shrimp
Fiddler crab
Fingernail clam
Flat mud crab
Flat oyster
Flatworm
Fluke, parasitic
Grass shrimp

Anadara transversa
Macoma balthica
Balanus spp.
Panopeus herbstii
Callinectes sapidus
Mytilus edulis
Rangia cuneata
Artemia spp.
Edwardsia elegans
Hexagenia spp.
Tricoptera spp.
Brachycentrus spp.
Acartia tonsa
Eurytemora affinis
Stylochus ellipticus
Busycon canaliculatum
Ancistrocoma pelseneeri
Nemopsis bachei
Obelia spp.
Mnemiopsis leidyi
Macrobdella grossa
Mulinia lateralis
Carcinonemertes carcinophilia
Acanthocyclops vernalis
Cyclops bicuspidatus thomasi
Cyclops spp.
Ergasilus clupeiदारु
Crassostrea virginica
Odostomia spp.
Neopanope sayi
Daphnia spp.
Uca spp.
Sphaeriidae spp.
Eurypanopeus depressus
Ostrea edulis
Paravortes gemellipara
Ribeiroia ondantrae
Palaemonetes pugio, *P. vulgaris*

Hard clam
Hermit crab
Hooked mussel
Horseshoe crab
Jingle shell
Marsh periwinkle
Moon jellyfish
Moon snail
Mud crab
Mud snails
Mysid
Pacific oyster
Parasitic brachyuran
Parasitic copepod
Parasitic copepod
Parasitic nematode
Pea crab
Razor clam
Ribbed mussel
Ribbon worm
Sand shrimp
Sea anemone
Sea grapes
Sea nettle
Sea star
Snapping shrimp
Softshell clam
Spiny-headed worm
Tapeworm
Thick-lipped oyster drill
Water flea
Water flea
Water flea
Water flea
Water flea
Whip mud worm
White-fingered mud crab

Mercenaria mercenaria
Pagurus spp.
Isbadium recurvum
Limulus polyphemus
Anomia simplex
Littorina irrorata
Aurelia aurita
Polinices duplicatus
Neopanope texana
Ilyanassa obsoleta
Neomysis americana
Crassostrea gigas
Argulus spp.
Myocheres major
Mycicola metensis
Ascaris spp.
Pinnotheres maculatus
Ensis directus
Geukensia demissa
Cerebratulus lacteus
Crangon septemspinosa
Diadumene leucolea
Mogula manhattensis
Chrysaora quinquecirrha
Asterias forbesi
Alpheus spp.
Mya arenaria
Echinorhynchus acus
Scolex polymorphus
Eupleura caudata
Bosmina longirostris
Daphnia magna
Daphnia pulex
Daphnia spp.
Holopedium giggerum
Polydora spp.
Rhithropanopeus harrissi

VERTEBRATES

Cartilaginous Fish

Bull shark	<i>Carcharhinus falciformis</i>	Skate	<i>Raja</i> spp.
Cownose ray	<i>Rhinoptera bonasus</i>	Smooth dogfish	<i>Mustelus canis</i>
Sandbar shark	<i>Carcharhinus plumbeus</i>		

Bony Fish

Alewife	<i>Alosa pseudoharengus</i>	Oyster toadfish	<i>Opsanus tau</i>
American eel	<i>Anguilla rostrata</i>	Pollock	<i>Pollachius virens</i>
American shad	<i>Alosa sapidissima</i>	Puffer	<i>Spaeroides maculatus</i>
Anchovy	<i>Anchoa</i> spp.	Pumpkinseed	<i>Lepomis gibbosus</i>
Atlantic croaker	<i>Micropogonias undulatus</i>	Red drum	<i>Sciaenops ocellatus</i>
Atlantic salmon	<i>Salmo salar</i>	Salmonids	<i>Salmo</i> and <i>Oncorhynchus</i> spp.
Atlantic silverside	<i>Menidia menidia</i>		
Bay anchovy	<i>Anchoa mitchilli</i>	Satinfin shiner	<i>Notropis amoenus</i>
Black crappie	<i>Pomoxis nigromaculatus</i>	Sculpins	<i>Cottidae</i> spp.
Black drum	<i>Pogonias cromis</i>	Sea lamprey	<i>Petromyzon marinus</i>
Blueback herring	<i>Alosa aestivalis</i>	Silver perch	<i>Bairdiella chrysoura</i>
Bluefish	<i>Pomatomus saltatrix</i>	Silverside	<i>Menidia</i> spp.
Bluegill	<i>Lepomis macrochirus</i>	Smelt	<i>Osmerus mordax</i>
Brown bullhead	<i>Ictalurus nebulosus</i>	Spanish mackerel	<i>Scomberomorus maculatus</i>
Carp	<i>Cyprinus carpio</i>	Speckled trout	<i>Cynoscion nebulosus</i>
Catfish	<i>Ictalurus</i> spp.	Spot	<i>Leiostomus xanthurus</i>
Chain pickerel	<i>Esox niger</i>	Spottail shiner	<i>Notropis hudsonius</i>
Channel catfish	<i>Ictalurus punctatus</i>	Striped anchovy	<i>Anchoa hepsetus</i>
Cobia	<i>Rachycentron canadum</i>	Striped bass	<i>Morone saxatilis</i>
Cutthroat trout	<i>Salmo clarki</i>	Striped killifish	<i>Fundulus majalis</i>
Freshwater lamprey	<i>Ichthyomyzon</i> spp.	Summer flounder	<i>Paralichthys dentatus</i>
Gar	<i>Lepisosteus</i> spp.	Sunfish	<i>Lepomis</i> spp.
Gizzard shad	<i>Dorosoma cepedianum</i>	Tautog	<i>Tautoga onitis</i>
Grass pickerel	<i>Esox vermiculatus</i>	Tessellated darter	<i>Etheostoma olmstedii</i>
Harvestfish	<i>Peprilus alepidotus</i>	Threadfin shad	<i>Dorosoma petenensis</i>
Hickory shad	<i>Alosa mediocris</i>	Tuna	<i>Thunnus</i> spp.
Hogchoker	<i>Trinectes maculatus</i>	Walleye	<i>Stizostedion vitreum vitreum</i>
Johnny darter	<i>Etheostoma nigrum</i>		
Killifish	<i>Fundulus</i> spp.	Weakfish	<i>Cynoscion regalis</i>
Lake trout	<i>Salvelinus namaycush</i>	White catfish	<i>Ictalurus catus</i>
Largemouth bass	<i>Micropterus salmoides</i>	White crappie	<i>Pomoxis annularis</i>
Longnose sucker	<i>Catostomus catostomus</i>	White bass	<i>Morone chrysops</i>
Large-scale sucker	<i>Catostomus macrocheilus</i>	White perch	<i>Morone americana</i>
Menhaden	<i>Brevoortia tyrannus</i>	Winter flounder	<i>Pleuronectes americanus</i>
Mummichog	<i>Fundulus heteroclitus</i>		
Northern pike	<i>Esox lucius</i>	Yellow perch	<i>Perca flavescens</i>
Northern redhorse	<i>Moxostoma aureolum</i>	Mosquitofish	<i>Gambusia affinis holbrooki</i>
Northern squawfish	<i>Ptychocheilus oregonensis</i>		

Reptiles

Atlantic ridley turtle	<i>Lepidochelys kempi</i>	Loggerhead turtle	<i>Caretta caretta caretta</i>
Black rat snake	<i>Elaphe obsoleta obsoleta</i>	Snapping turtle	<i>Chelydra serpentina</i>
Gray rat snake	<i>Elaphe obsoleta spiloides</i>		

Birds

American crow	<i>Corvus brachyrhynchos</i>	Least tern	<i>Sterna antillarum</i>
American great egret	<i>Casmerodius albus</i>	Little blue heron	<i>Egretta caerulea</i>
American wigeon	<i>Anas americana</i>	Loon	<i>Gavia immer</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>	Magpie	<i>Pica pica</i>
Barn swallow	<i>Hirundo rustica</i>	Mallard	<i>Anas platyrhynchos</i>
Black duck	<i>Anas rubripes</i>	Mandarin duck	<i>Aix galericulata</i>
Black-crowned night heron	<i>Nycticorax nycticorax</i>	Northern flicker	<i>Colaptes auratus</i>
Blue-winged teal	<i>Anas discors</i>	Northern pintail	<i>Anas acuta</i>
California gull	<i>Larus californicus</i>	Oldsquaw	<i>Clangula byemalis</i>
Canada goose	<i>Branta canadensis</i>	Osprey	<i>Pandion haliaetus</i>
Canvasback	<i>Aythya valisneria</i>	Pileated woodpecker	<i>Dryocopus pileatus</i>
Cattle egret	<i>Bubulcus ibis</i>	Pochard, common	<i>Aythya ferina</i>
Common barn owl	<i>Tyto alba</i>	Red-tailed hawk	<i>Buteo jamaicensis</i>
Common grackle	<i>Quiscalus quiscula</i>	Red-winged blackbird	<i>Agelaius phoeniceus</i>
Common tern	<i>Sterna hirundo</i>	Redhead	<i>Aythya americana</i>
Eastern kingbird	<i>Tyrannus tyrannus</i>	Ring-necked duck	<i>Aythya collaris</i>
Egret	<i>Casmerodius</i> spp.	Ruddy duck	<i>Oxyura jamaicensis</i>
Fish crow	<i>Corvus ossifragus</i>	Scaup, greater	<i>Aythya marila</i>
Golden eagle	<i>Aquila chrysaetos</i>	Scaup, lesser	<i>Aythya affinis</i>
Goldeneye, common	<i>Bucephala clangula</i>	Scoter	<i>Melanitta</i> spp.
Great black-backed gull	<i>Larus marinus</i>	Snowy egret	<i>Egretta thula</i>
Great blue heron	<i>Ardea herodias</i>	Starling	<i>Sturnus vulgaris</i>
Great horned owl	<i>Bubo virginianus</i>	Tern	<i>Sterna</i> spp.
Green heron	<i>Butorides striatus</i>	Tricolored heron	<i>Egretta tricolor</i>
Green-backed heron	<i>Butorides striatus</i>	Tundra swan	<i>Cygnus columbianus</i>
Herring gull	<i>Larus argentatus</i>	Turkey vulture	<i>Cathartes aura</i>
Horned grebe	<i>Podiceps auritus</i>	Wood duck	<i>Aix sponsa</i>
House sparrow	<i>Passer domesticus</i>	Yellow-crowned night heron	<i>Nycticorax violaceus</i>

Mammals

Beaver	<i>Castor canadensis</i>	Norway rat	<i>Rattus norvegicus</i>
Coyote	<i>Canis latrans</i>	Raccoon	<i>Procyon lotor</i>
Grey fox	<i>Urocyon cinereoargenteus</i>	Red fox	<i>Vulpes vulpes</i>
Mink	<i>Mustela vison</i>	Striped skunk	<i>Mephitis mephitis</i>
Muskrat	<i>Ondatra zibethicus</i>	White-tailed deer	<i>Odocoileus virginianus</i>

OTHER ORGANISMS

Bacterium	<i>Actinobacillus</i> spp.	Crab fungal parasite	<i>Lagenidium callinectes</i>
Bacterium	<i>Aeromonas liquefaciens</i>	Dermo, oyster disease	<i>Perkinsus marinus</i>
Bacterium	<i>Flexibacter columnaris</i>	MSX, oyster disease	<i>Haplosporidium nelsoni</i>
Bacterium	<i>Staphylococcus</i> spp.	SSO, oyster disease	<i>Haplosporidium costale</i>
Bacterium	<i>Streptococcus</i> spp.	Toxic dinoflagellate	<i>Protogonyaulax</i>
Bacterium	<i>Vibrio anguillarum</i>		<i>tamarensis</i>

LIST OF ABBREVIATIONS

BOD	biochemical oxygen demand	LT ₅₀	lethal time of exposure resulting in 50 percent mortality
BPI	breeding population index	lux	a unit of light intensity
C	celsius	m	meter
Chl	chlorophyll	m ²	per square meter
cm	centimeter	m ³	per cubic meter
cm s ⁻¹	centimeters per second	mg O ₂ L ⁻¹	milligrams of oxygen per liter (parts per million)
CPO	chlorine-produced oxidants (compounds formed by reactions of chlorine used for water disinfection with other contaminants in water)	mgL ⁻¹	milligrams per liter (parts per million)
CPUE	catch per unit effort	mg g ⁻¹	milligrams per gram (parts per thousand)
dbh	diameter at breast height	mg kg ⁻¹	milligrams per kilogram (parts per million)
DDE	dichlorodiphenylchloroethane	ml ⁻¹	per milliliter
DDT	dichlorodiphenyltrichloroethane	mm d ⁻¹	millimeters per day
DIN	dissolved inorganic nitrogen	mm Hg	millimeters of mercury
DIP	dissolved inorganic phosphorus	mt DNA	mitochondrial deoxyribonucleic acid
DNA	deoxyribonucleic acid	n	number in sample population
DO	dissolved oxygen	NTA	nitritotriacetic acid
DVE	duck viral enteritis	NTU	nephelometric turbidity units
dynes cm ⁻²	dynes per square centimeter	O ₂	oxygen
EC ₅₀	concentration effecting specific response in 50 percent of test organisms	PAH	polynuclear aromatic hydrocarbon
FL	fork length	PCB	polychlorinated biphenyl
ft	feet	pH	log hydrogen ion concentration
g	gram	pO ₂	partial pressure of oxygen
gL ⁻¹	grams per liter (parts per thousand)	ppt	parts per thousand
ha	hectare	rm	river mile
h	hour	RSA	registered shooting area
IPNV	infectious pancreatic necrosis virus	SAV	submerged aquatic vegetation
kcal g ⁻¹	kilocalories per gram	SL	standard length
kcal	kilocalories	TBT	tributyltin
K _d	light attenuation coefficient	TBTO	tributyltin oxide
kg	kilogram	TL	total length
km	kilometer	TLm	Median tolerance limit (to a toxic substance or other stress factor; the level of the stressor at which half of the organisms tested show the measured response)
km ²	square kilometers	TSS	total suspended solids
L	liter	µg kg ⁻¹	micrograms per kilogram (parts per billion)
L ⁻¹	per liter	µgL ⁻¹	micrograms per liter (parts per billion)
lb	pounds	µg g ⁻¹	micrograms per gram (parts per million)
LC ₅₀	lethal concentration - 50 percent mortality	µm	micrometer
LD ₅₀	lethal dose for 50 percent of the test organisms		
LDH	lactate dehydrogenase, a digestive enzyme		
LS ₅₀	median lethal shear that would kill 50% of test animals		

MAP APPENDIX

Sources of map information

Peter Bergstrom
Computer Sciences Corporation
Chesapeake Bay Program Office
Annapolis, Maryland

The author(s) of each chapter were sent a copy of the map(s) for their species at 1:250,000 scale from the first edition of this report. The maps in the first edition were based primarily on 1:250,000 scale maps produced by Western Eco-systems Technology, Inc. for the U.S. Army Corps of Engineers' 1982 *Chesapeake Bay Low Freshwater Inflow Study* (Low Flow Study). The maps used were unpublished base maps dated 1980 representing "known and potential" distribution, not the maps published in the *Map Folio* as part of the Low Flow Study report series. The 1980 base maps were edited, based upon literature reports of actual habitat, and defined potential habitat (based on salinity, depth, and substrate preferences of the target species) to produce the habitat distribution maps found in the first edition of this report. The edited maps were digitized by Computer Sciences Corporation (CSC) staff contracted to the Environmental Protection Agency (EPA) at the Chesapeake Bay Program Office (CBPO), and plotted with an ARC/INFO Geographic Information System (GIS). The same system was used by CSC/CBPO staff to produce the revised maps in this volume.

In all cases, the authors revised the original maps for use in this volume. In many cases entirely new maps were generated (SAV, eastern oyster, soft shell and hard clams, spot, yellow perch, white perch adult, barriers to fish passage, low DO zones, and all the bird maps). In other cases, the authors edited the original map using new information. All authors were asked to delineate potential habitat, and to separately map actual current and historical habitat where possible. It was not always possible to achieve this goal, and for many species the distribution shown is a combination of actual and potential habitat. Because the original scale of most of the maps was 1:250,000, and the information for the maps came from a wide variety of sources, they should not be used for regulatory purposes, or to delineate species habitat on a more local scale (e.g., at 1:24,000).

Maps of bird habitats include data from surveys. The wintering waterfowl maps (Maps 36-38) include three-year running means of mid-winter aerial survey counts conducted by the U.S. Fish and Wildlife Service. The maps of breeding bird distributions (Maps 34-35, 39-46) all include data from Breeding Bird Atlas data bases maintained by the Virginia Department of Game and Inland Fisheries and Maryland Department of Natural Resources, Wildlife Division. These data were collected by volunteers who identified all the bird species nesting in blocks defined by one-sixth of a USGS "quad" or 1:24,000 topographic map. Only blocks with "confirmed" or "probable" breeding codes were used for these maps. Since no estimate of population size was made, and nest locations within the block were not recorded, the maps show the outline of each one-sixth quad block that had confirmed or probable breeding for that species during any of the years of data collection. For several target species there were no "probable" codes allowed, so only "confirmed" nesting blocks are shown. Maps of species with a high nesting density sometimes had blocks that appeared to have nests because all the adjoining blocks had nests; these were marked with an asterisk to show they did not have nests. Concentration areas in Map 46 (Bald eagle) were based on surveys of roosting areas.

Maps of colonial wading bird breeding habitats also show specific colony locations with 1988 population sizes. These data came from surveys conducted by researchers or state agency staff, done independently from the Breeding Bird Atlas surveys. Only 1988 colony sizes are shown because that year had the most complete data. Each known colony has a 10 km foraging radius shown, which includes most of the foraging habitat used by nesting adults in the species that have been studied.

In some cases, data for the maps came from the Chesapeake Bay Program data base. Map 7 (SAV species) and Maps 23-26 (Spot) were based, in part, on bathymetry data. In Map 28 (white perch adult) salinity data was used

to define the down stream limit of distribution. Map 33 (Dissolved Oxygen) is based on monitoring data.

The Dissolved Oxygen map (Map 33) shows areas from which several target species are currently excluded due to their intolerance of low DO, or the absence of prey species. Data from fixed stations in the mainstem of the Bay collected during the summer (July-September) of 1985-1989 were spatially interpolated using an inverse squared distance three-dimensional interpolator. Means of the interpolated dissolved oxygen values were calculated over all years and all below pycnocline depths, and areas with mean DO below 3 and 2 mgL⁻¹ are shown. Low summer DO occurs in some tributaries, but was not mapped.

Acknowledgements

Digitizing and map editing and production were done by Marisa Capriotti and Danny Elliott, supervised by Lynda Liptrap (all CSC/CBPO staff). Lowell Bahner (CSC/CBPO) calculated the mean dissolved oxygen values for Map 33. Lettering, additional shading, and final layout were done by Fishergate, Inc. Helpful comments on map design and content came from Kent Mountford (EPA/CBPO), Steve Funderburk and Doug Forsell (USFWS), and Steve Jordan, Cynthia Stenger, and Lamar Platt (MDNR). All the authors are acknowledged for their efforts to provide and check map information. Map editing and production was funded by the U.S. Environmental Protection Agency, Chesapeake Bay Program.

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Habitat distribution in the Chesapeake Bay

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Habitat distribution of adults in the Chesapeake Bay

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Habitat distribution of spawning and nursery areas in the Chesapeake Bay

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Habitat distribution of spawning and nursery areas in the Chesapeake Bay

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Nesting habitats in the Chesapeake Bay region, 1982-1989

45 Osprey *Pandion haliaetus*

Nesting habitats in the Chesapeake Bay region, 1982-1989

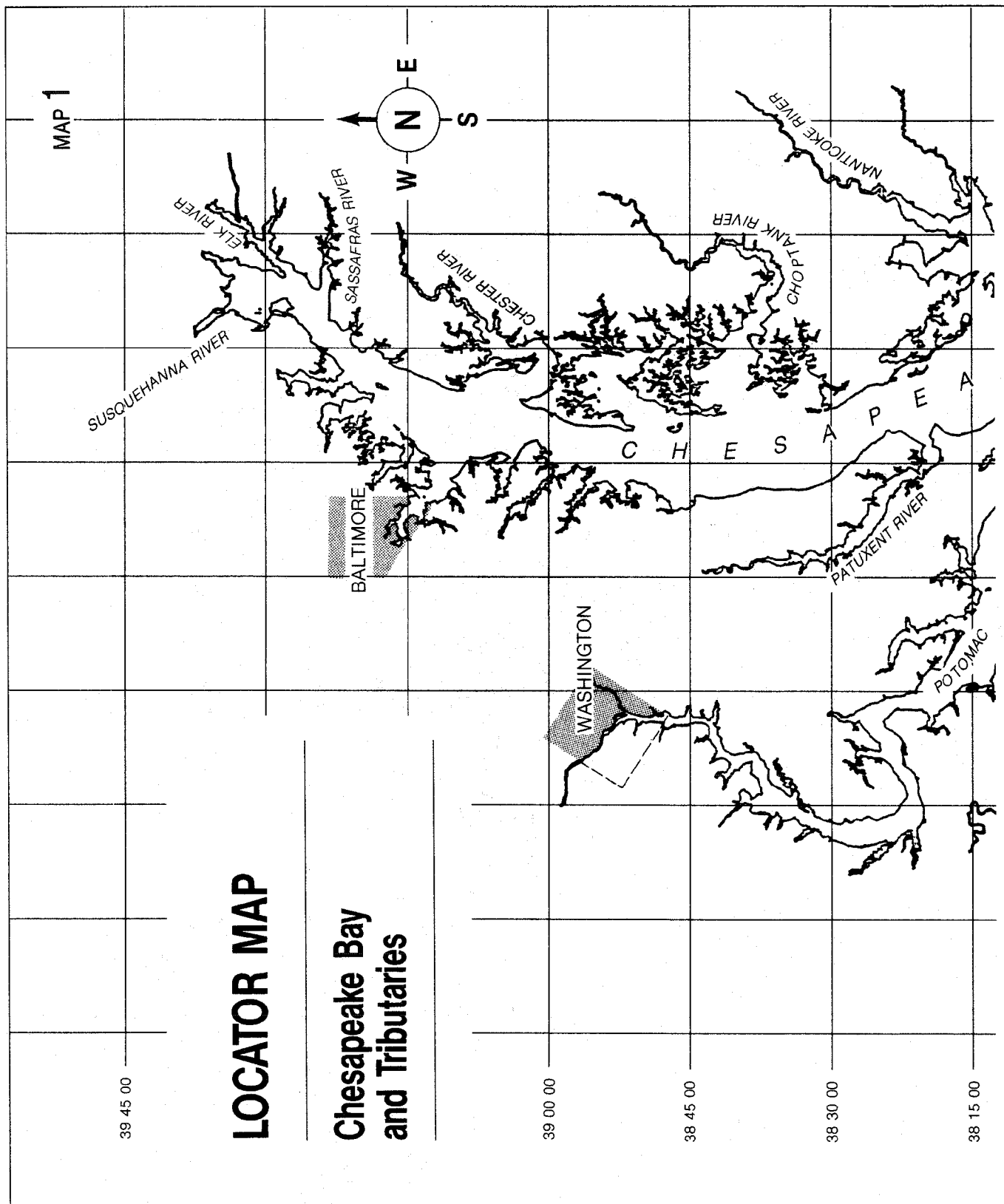
46 Bald eagle *Haliaeetus leucocephalus*

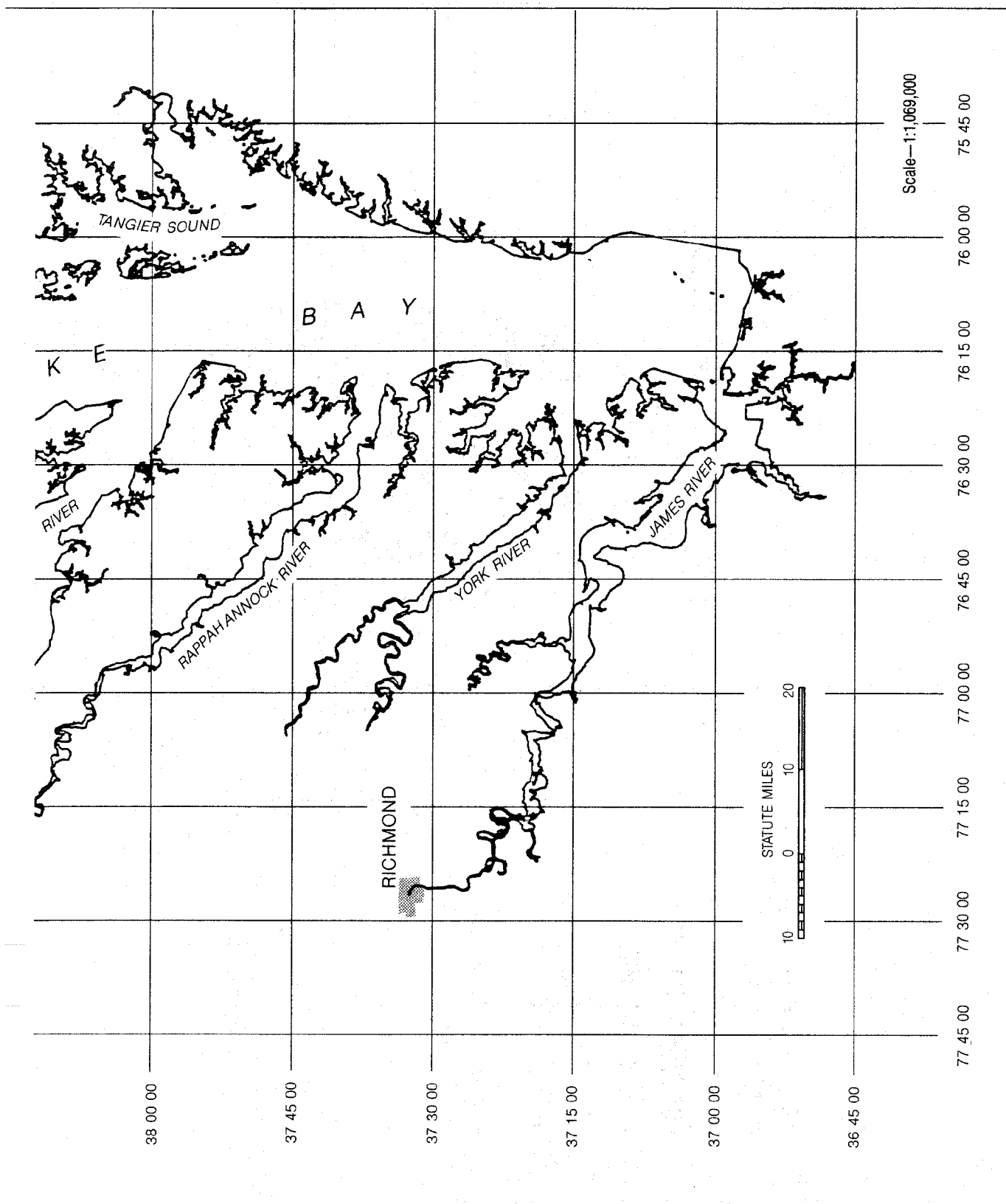
Nesting habitats in the Chesapeake Bay region, 1982-1990

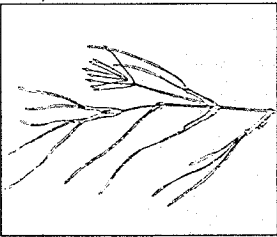
47 Bald eagle *Haliaeetus leucocephalus*

Potential habitat and concentration areas in the Chesapeake Bay region

MAPS





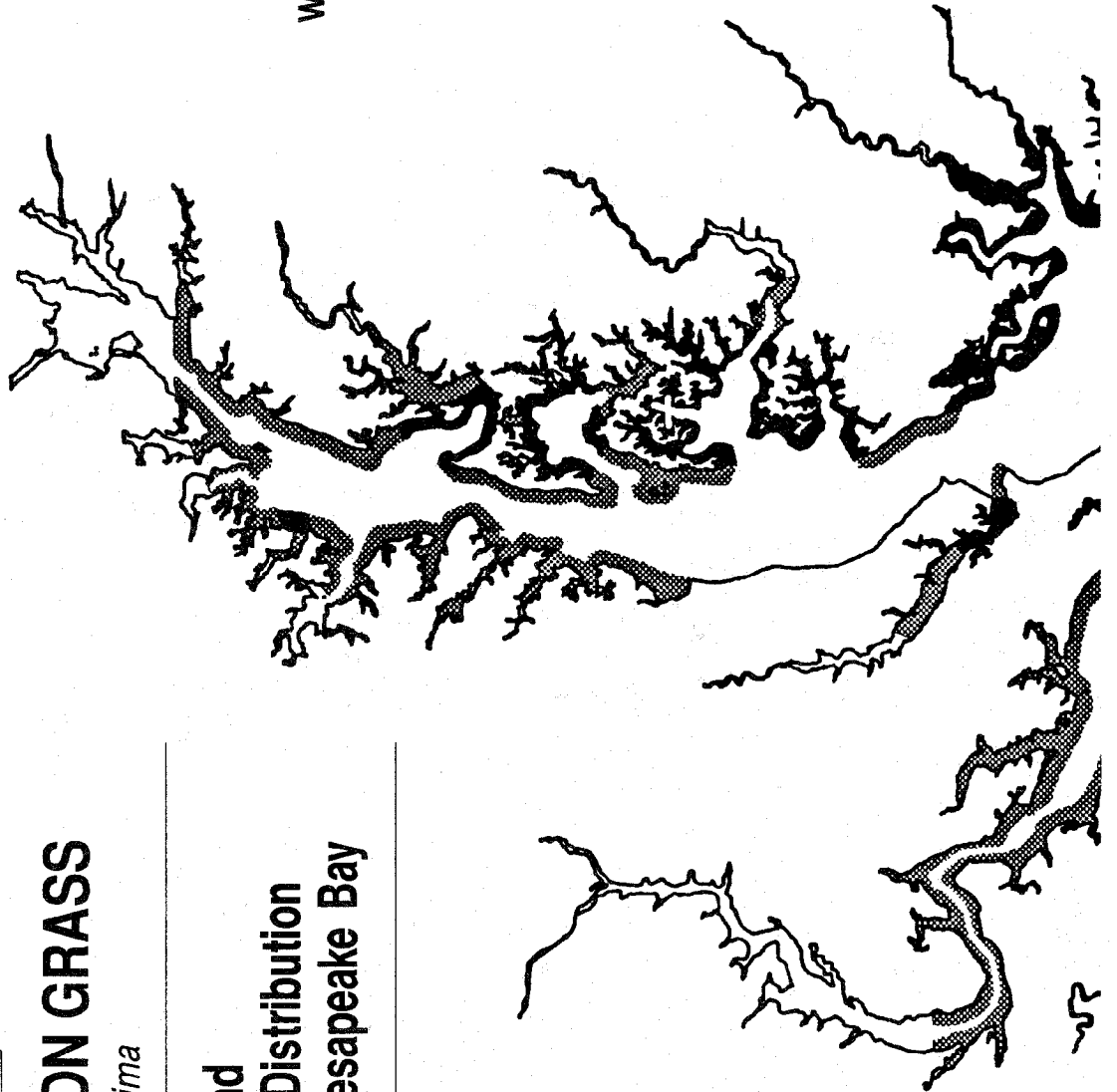
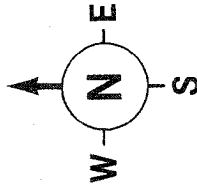


WIDGEON GRASS

Ruppia maritima

Recent and
Potential Distribution
in the Chesapeake Bay

MAP 2

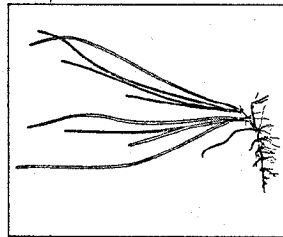




SOURCE: General distribution based on aerial surveys, (recent distribution) and salinity and substrate preferences (potential distribution). Some areas deeper than the usual depth limit (2 meters) are shaded; see Map 7 (SAV species) for more accurate depth limits.

Potential distribution
Recent distribution

Scale—1:1,069,000

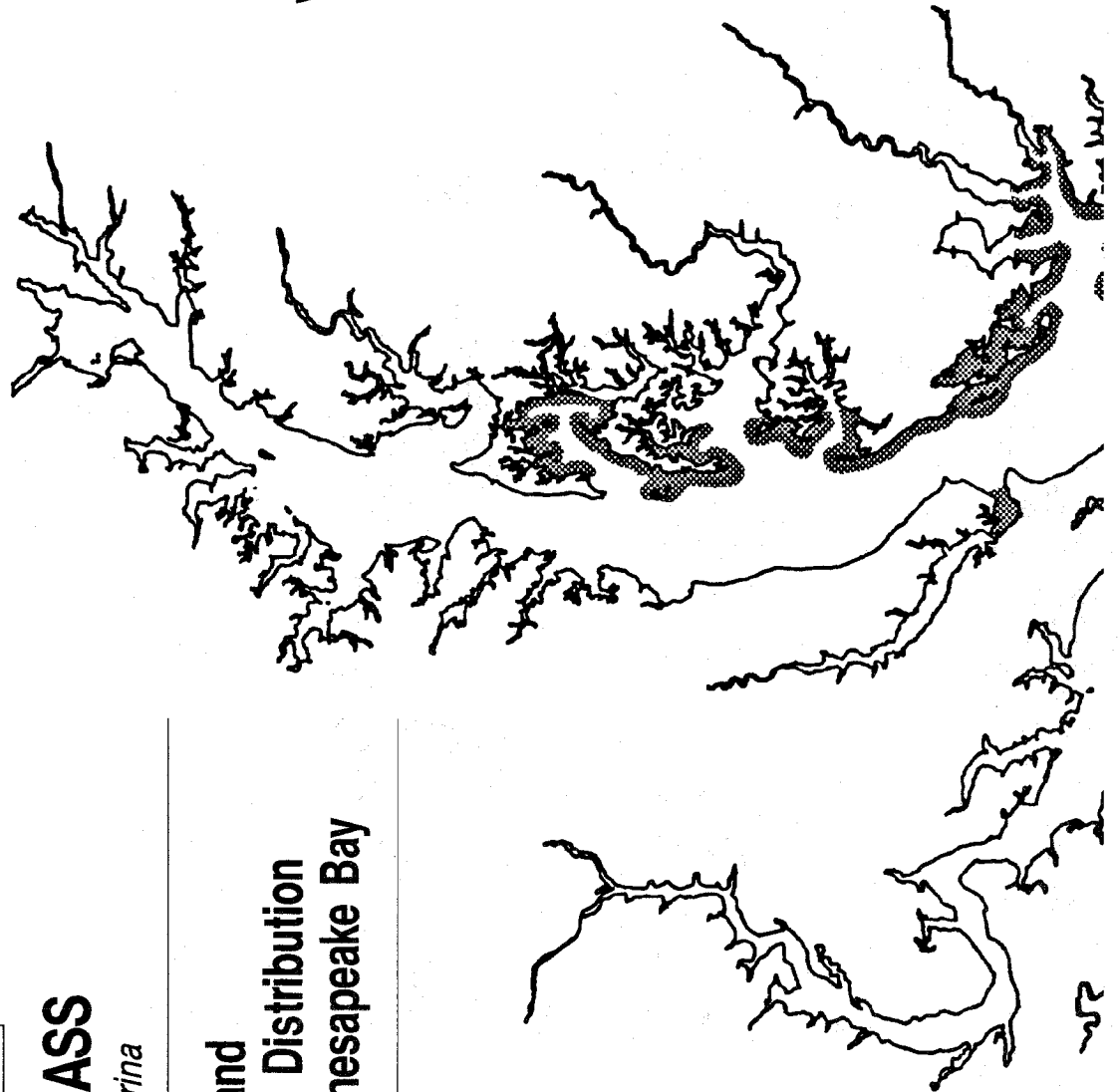
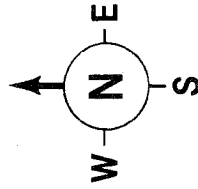


EELGRASS



Zostera marina

Recent and Potential Distribution in the Chesapeake Bay

MAP 3

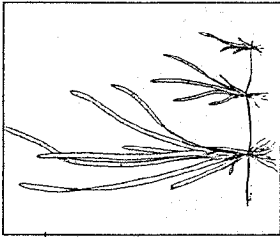




 Potential distribution
 Recent distribution

SOURCE: General distribution based on aerial surveys (recent distribution) and salinity and substrate preferences (potential distribution). Some areas deeper than the usual depth limit (2 meters) are shaded; see Map 7 (SAV species) for more accurate depth limits.

Scale—1:1,069,000

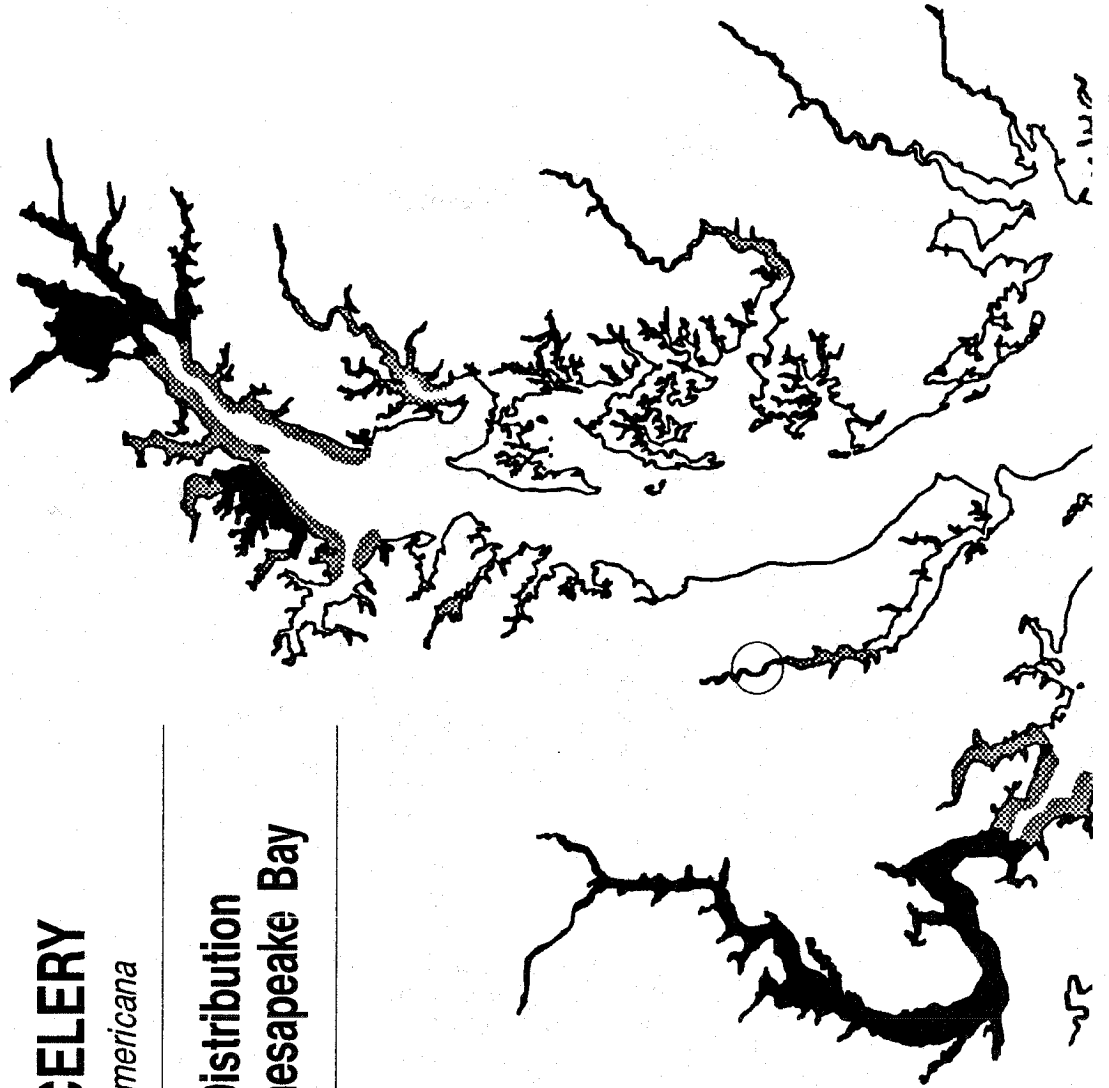
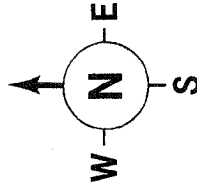


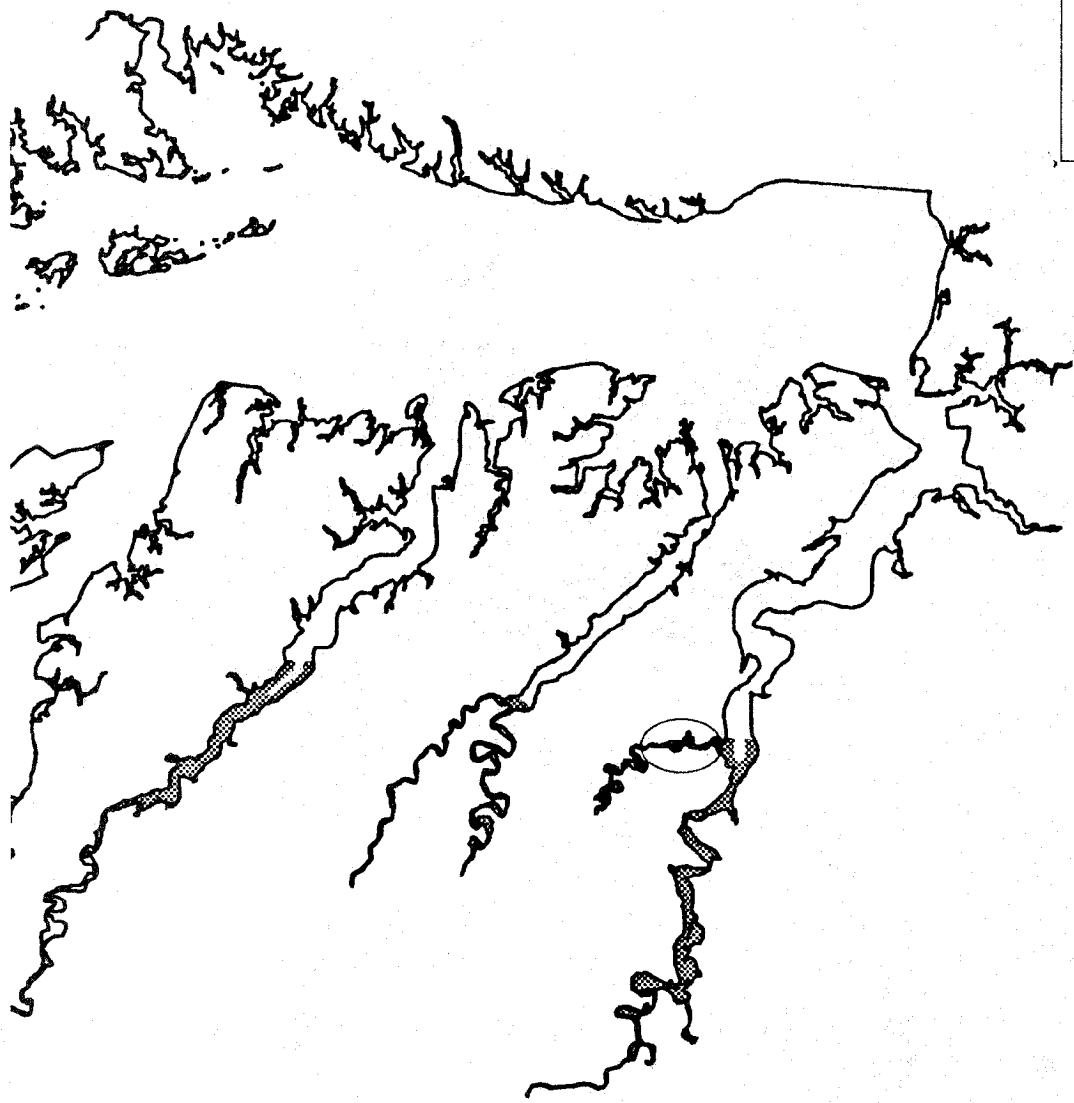
WILD CELERY

Vallisneria americana

Habitat Distribution in the Chesapeake Bay

MAP 4

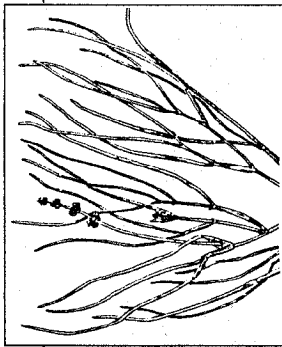




SOURCE: General distribution based on aerial surveys (recent distribution) and salinity and substrate preferences (potential distribution). Some areas deeper than the usual depth limit (2 meters) are shaded; see Map 7 (SAV species) for more accurate depth limits.

Potential distribution
or Recent distribution

Scale—1:1,069,000

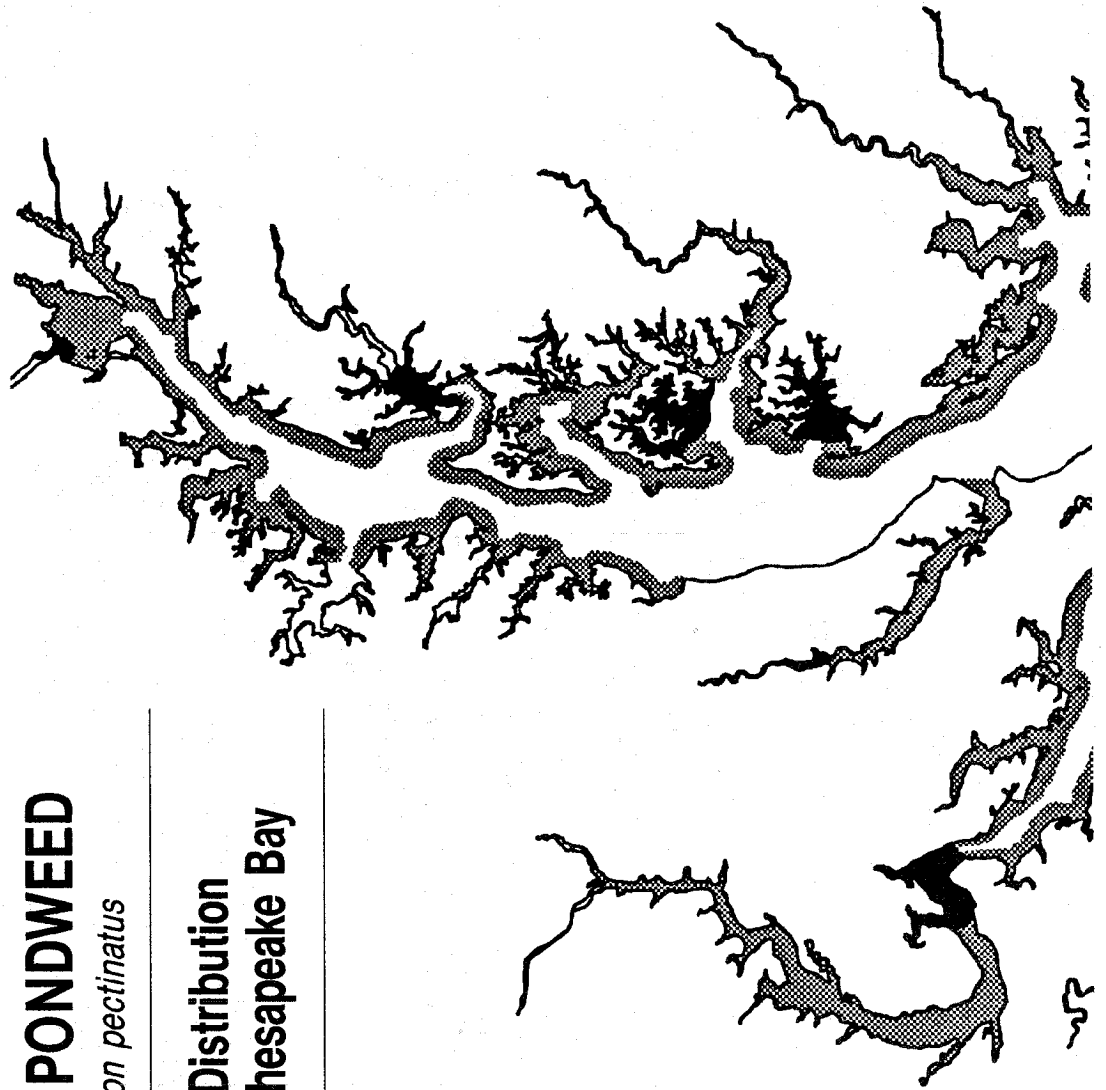
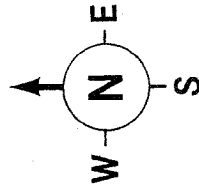


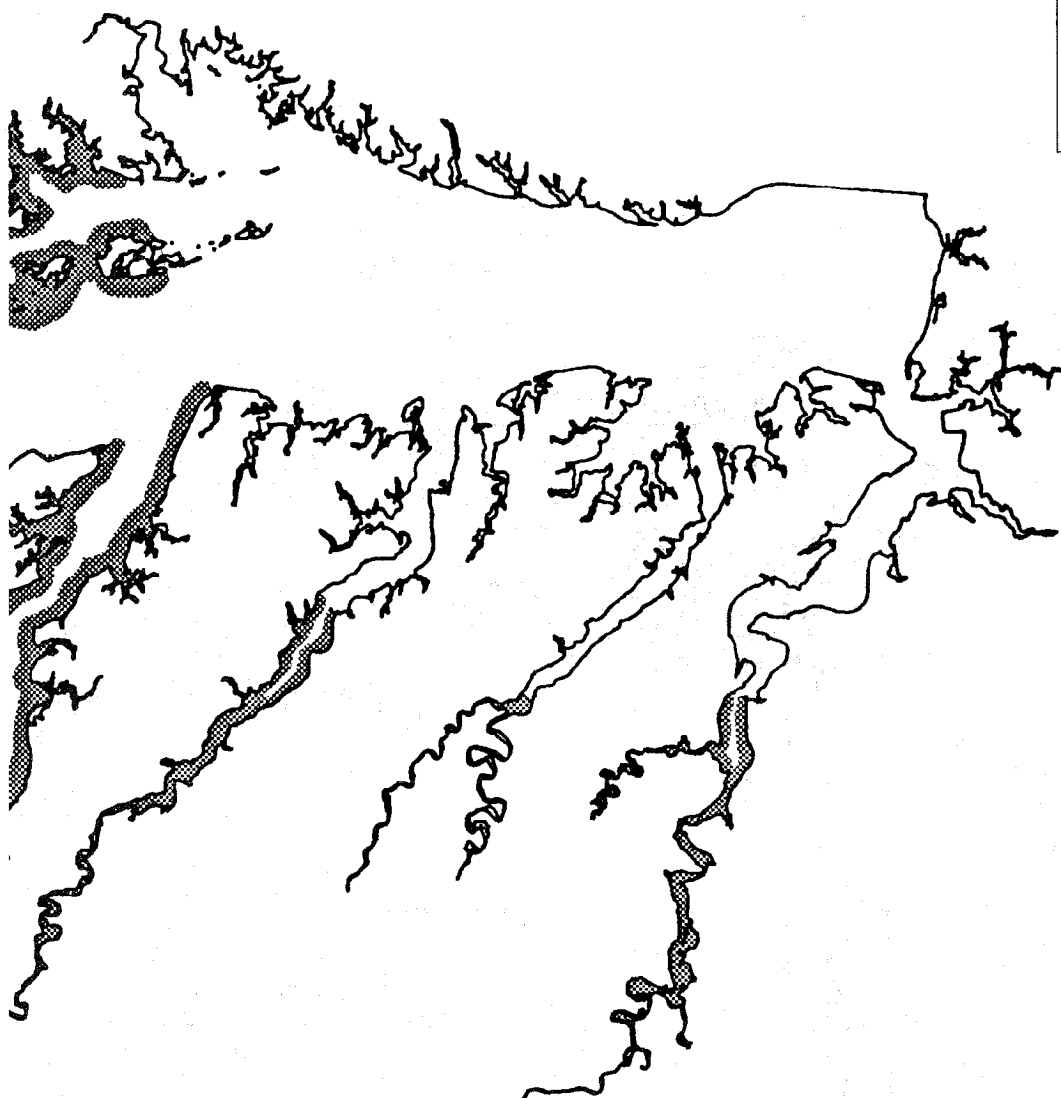
SAGO PONDWEED

Potamogeton pectinatus

Habitat Distribution in the Chesapeake Bay

MAP 5





SOURCE: General distribution based on aerial surveys (recent distribution) and salinity and substrate preferences (potential distribution). Some areas deeper than the usual depth limit (2 meters) are shaded; see Map 7 (SAV species) for more accurate depth limits.

Potential distribution
Recent distribution

Scale — 1:1,069,000

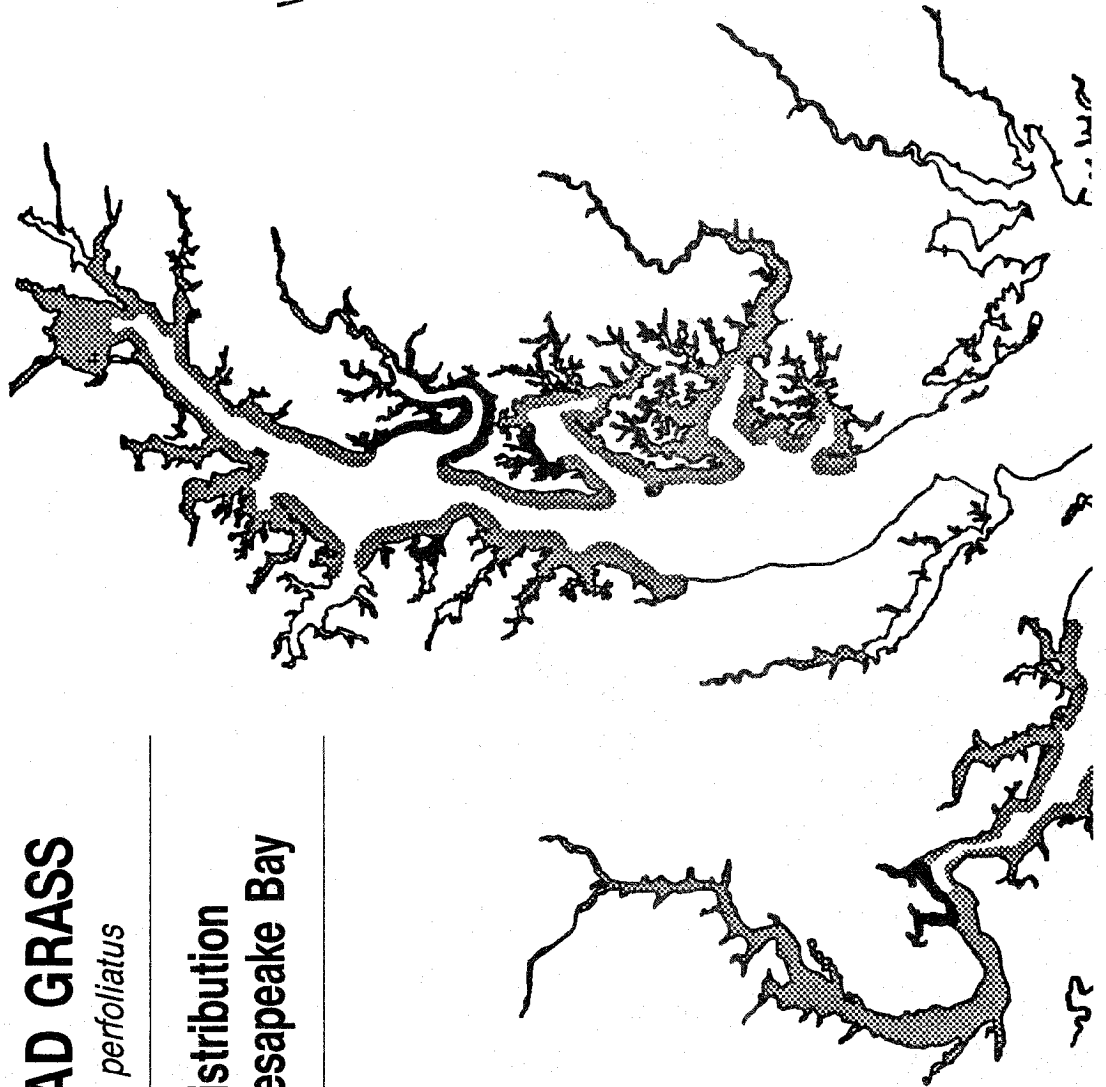
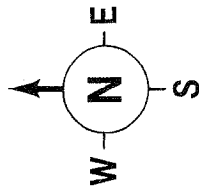


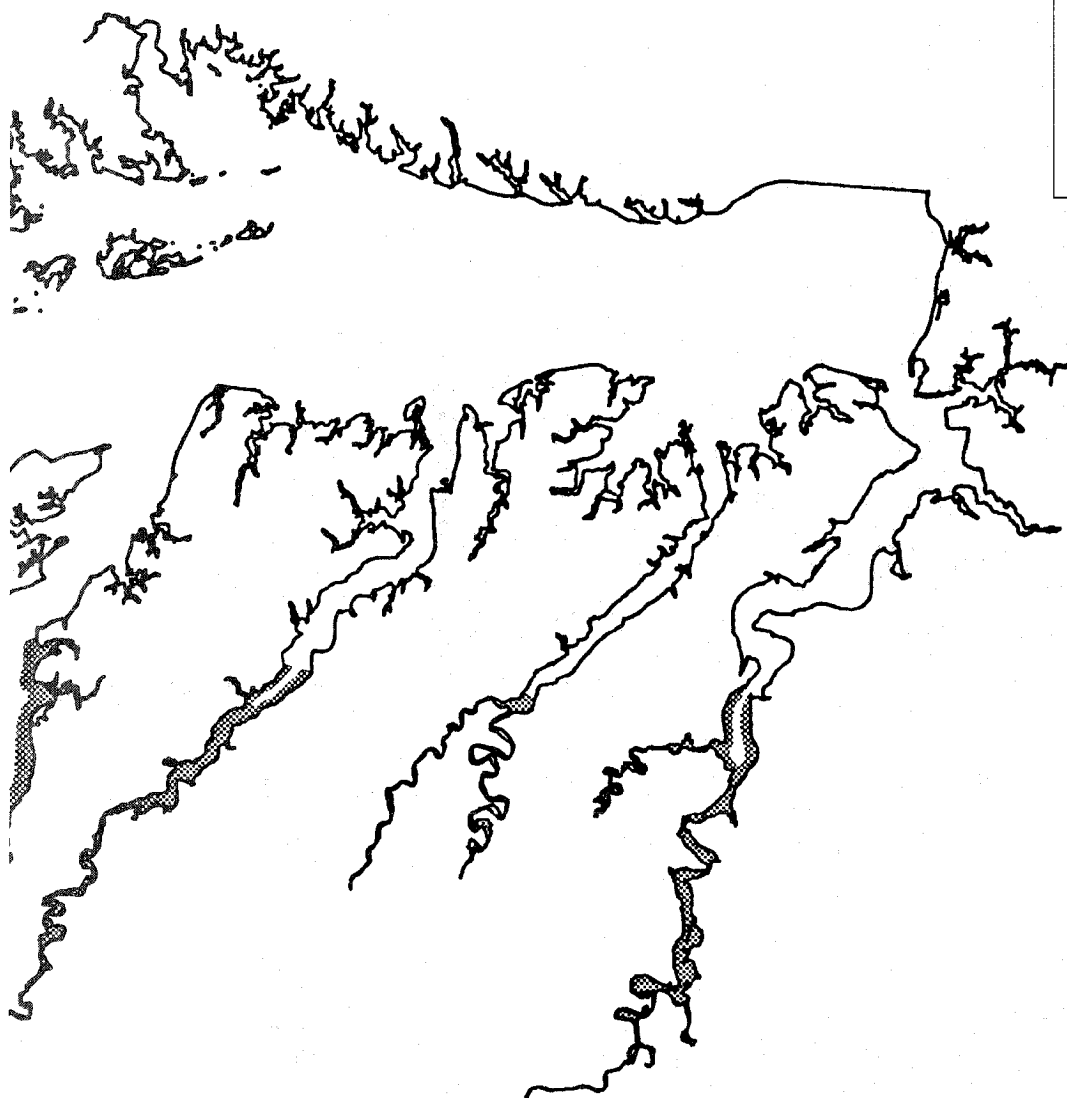
REDHEAD GRASS

Potamogeton perfoliatus



Habitat Distribution
in the Chesapeake Bay

MAP 6

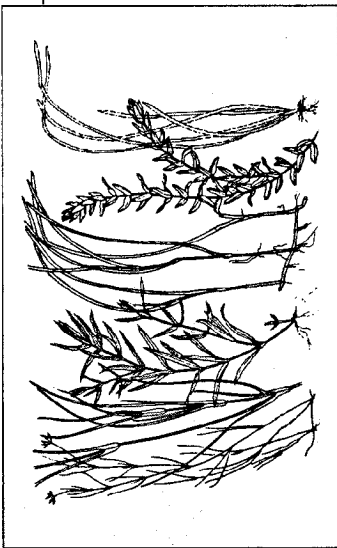




SOURCE: General distribution based on aerial surveys (recent distribution) and salinity and substrate preferences (potential distribution). Some areas deeper than the usual depth limit (2 meters) are shaded; see Map 7 (SN species) for more accurate depth limits.

 Potential distribution
 Recent distribution

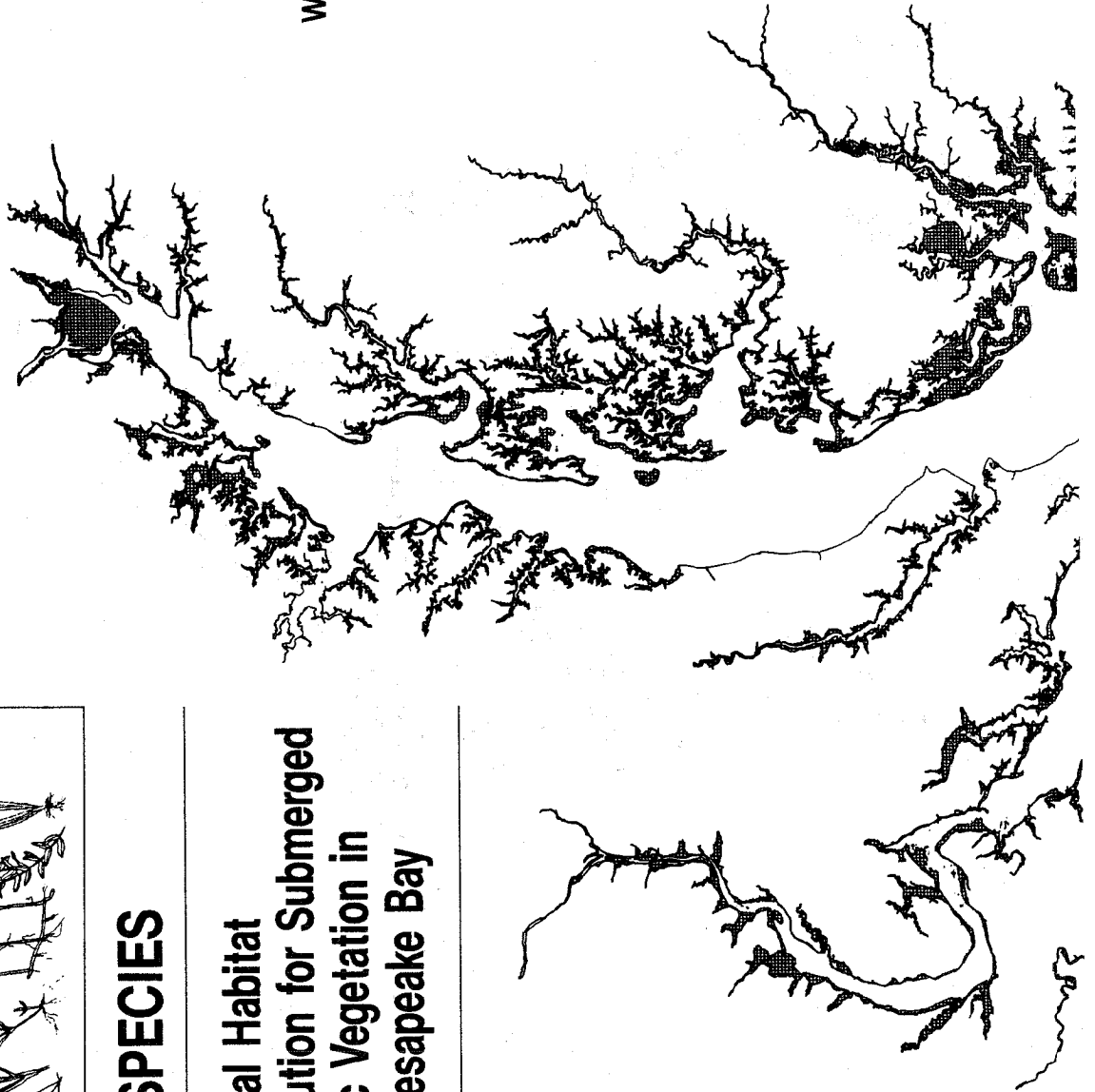
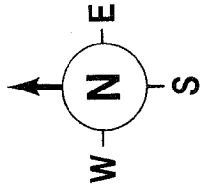
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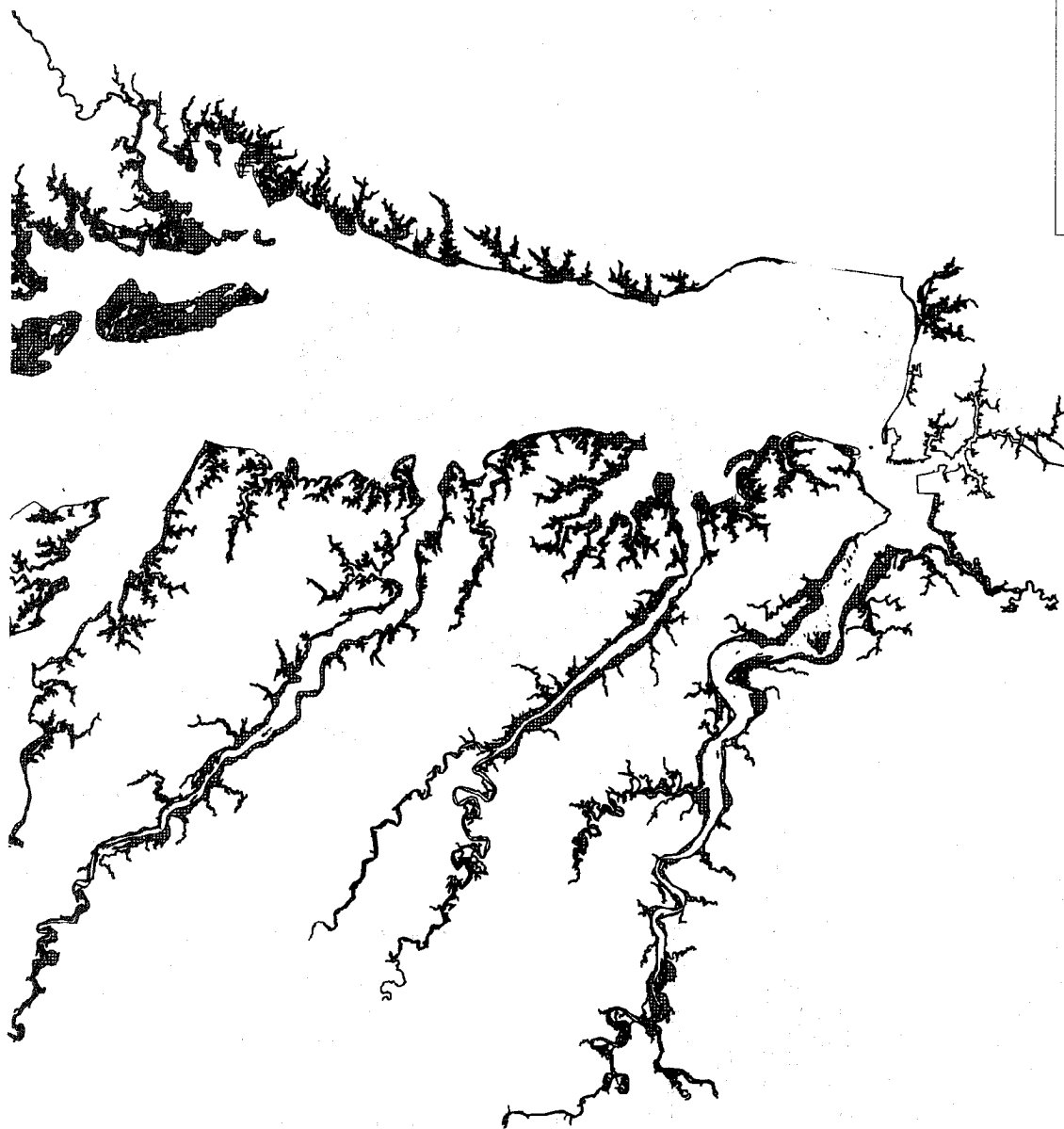


SAV SPECIES

Potential Habitat
Distribution for Submerged
Aquatic Vegetation in
the Chesapeake Bay

MAP 7





■ Potential habitat for
any SAV species

SOURCE: Two meter depth contour, minus
any areas of unsuitable habitat (due
to substrate, currents, etc.).

Scale—1:1,069,000

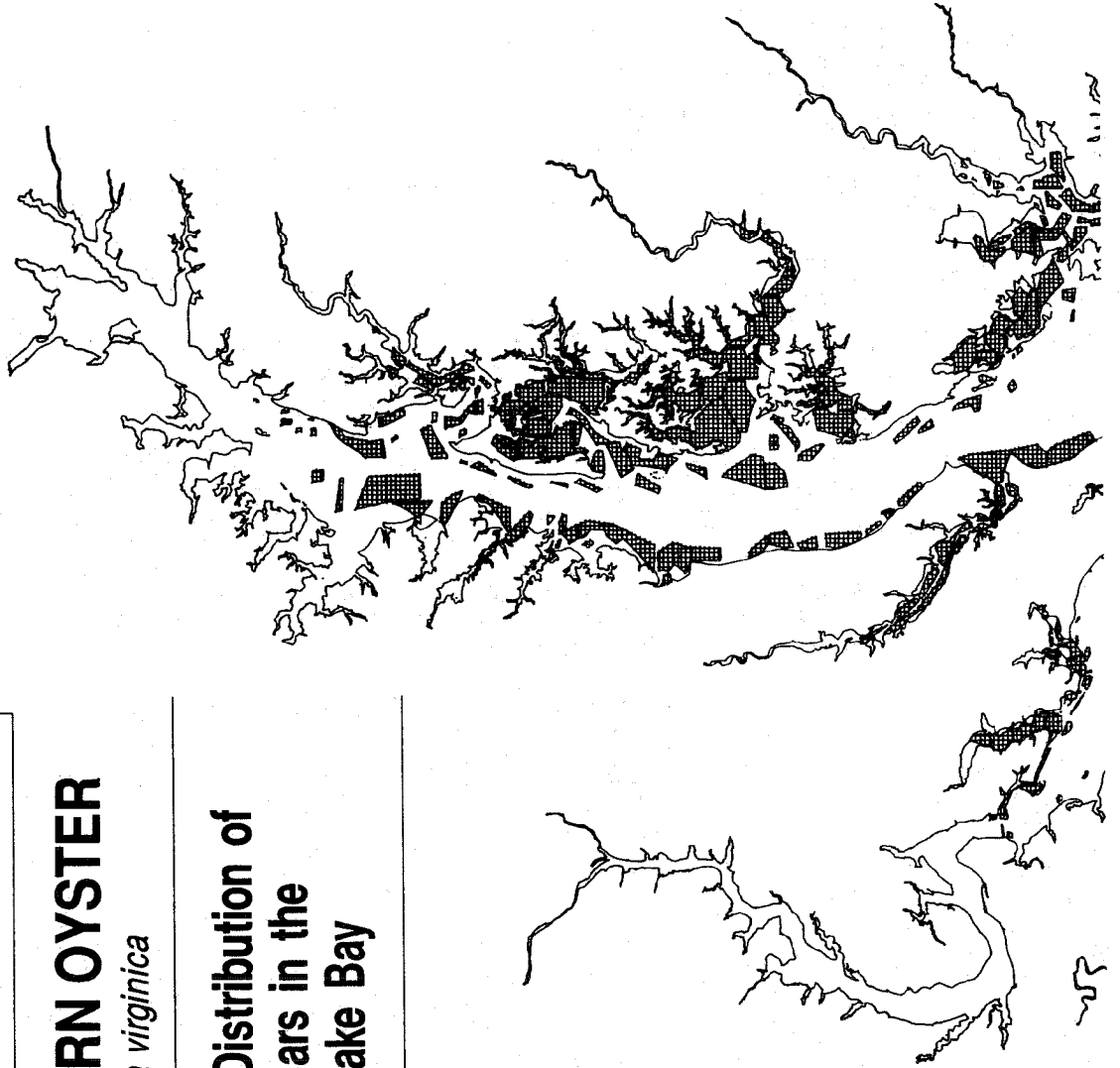
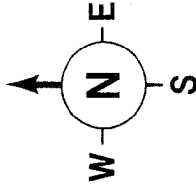


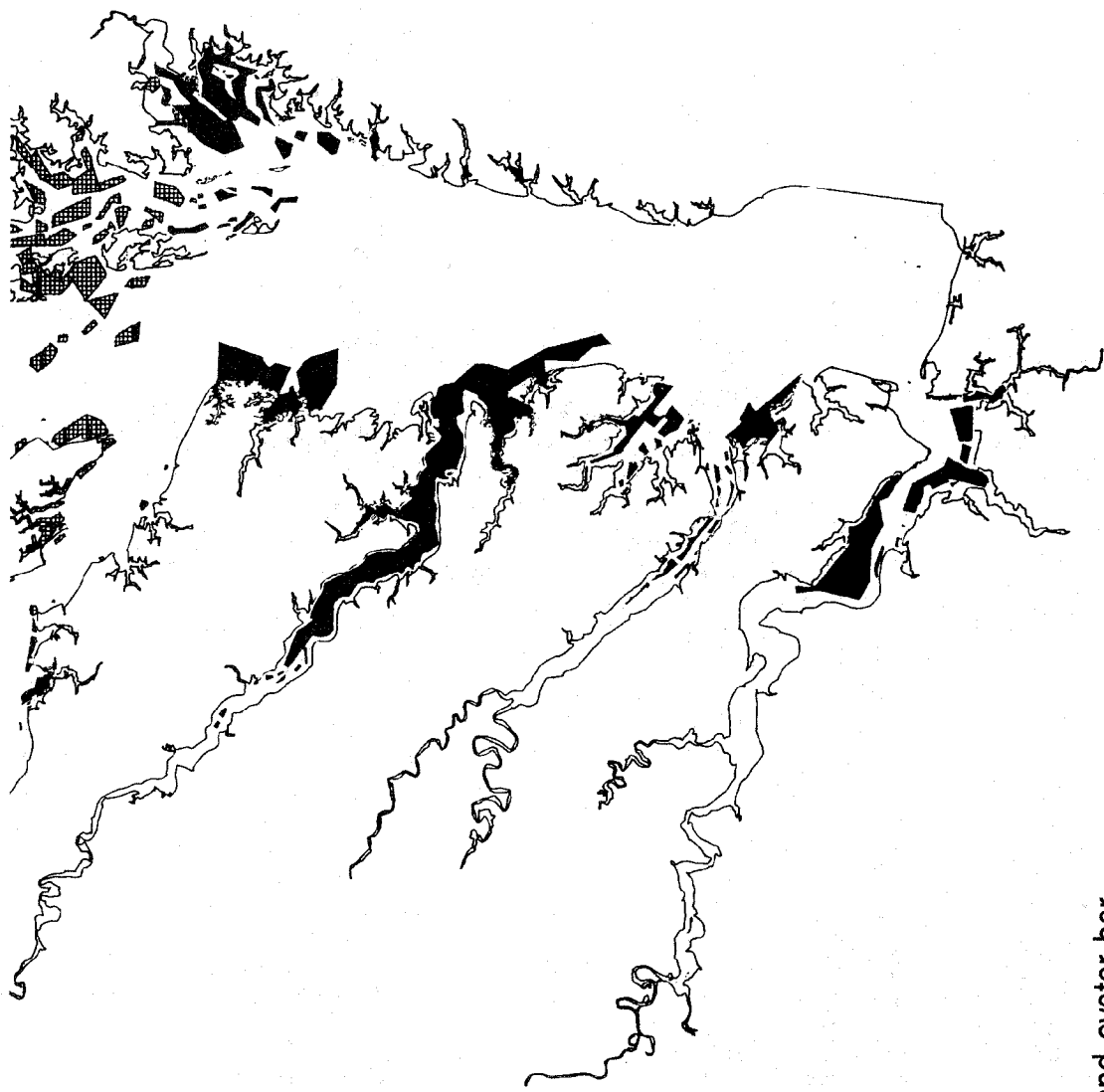
EASTERN OYSTER

Crassostrea virginica

Habitat Distribution of Oyster Bars in the Chesapeake Bay

MAP 8



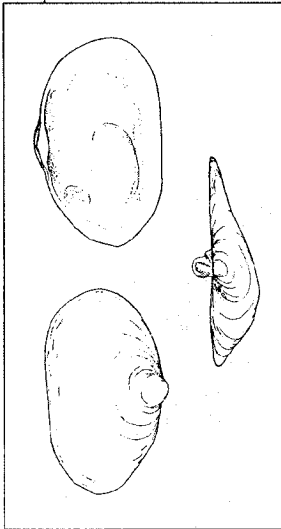
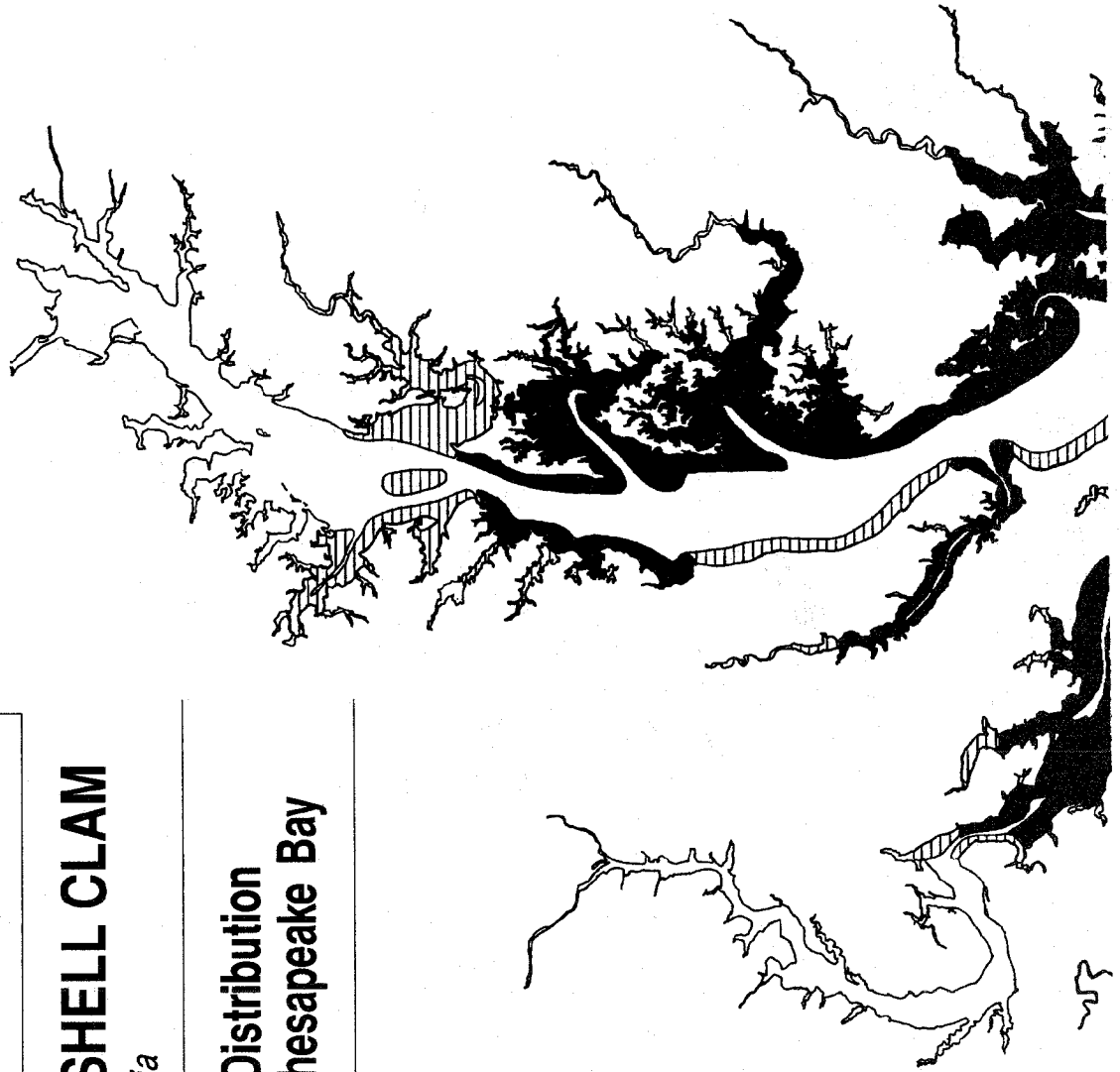
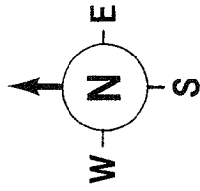


■ Maryland oyster bar locations
■ Virginia oyster bar locations

SOURCES: MD—1983 DNR seed site survey, VA—1909 Baylor grounds. (Both are potential, not actual habitat.)

Scale—1:1,069,000

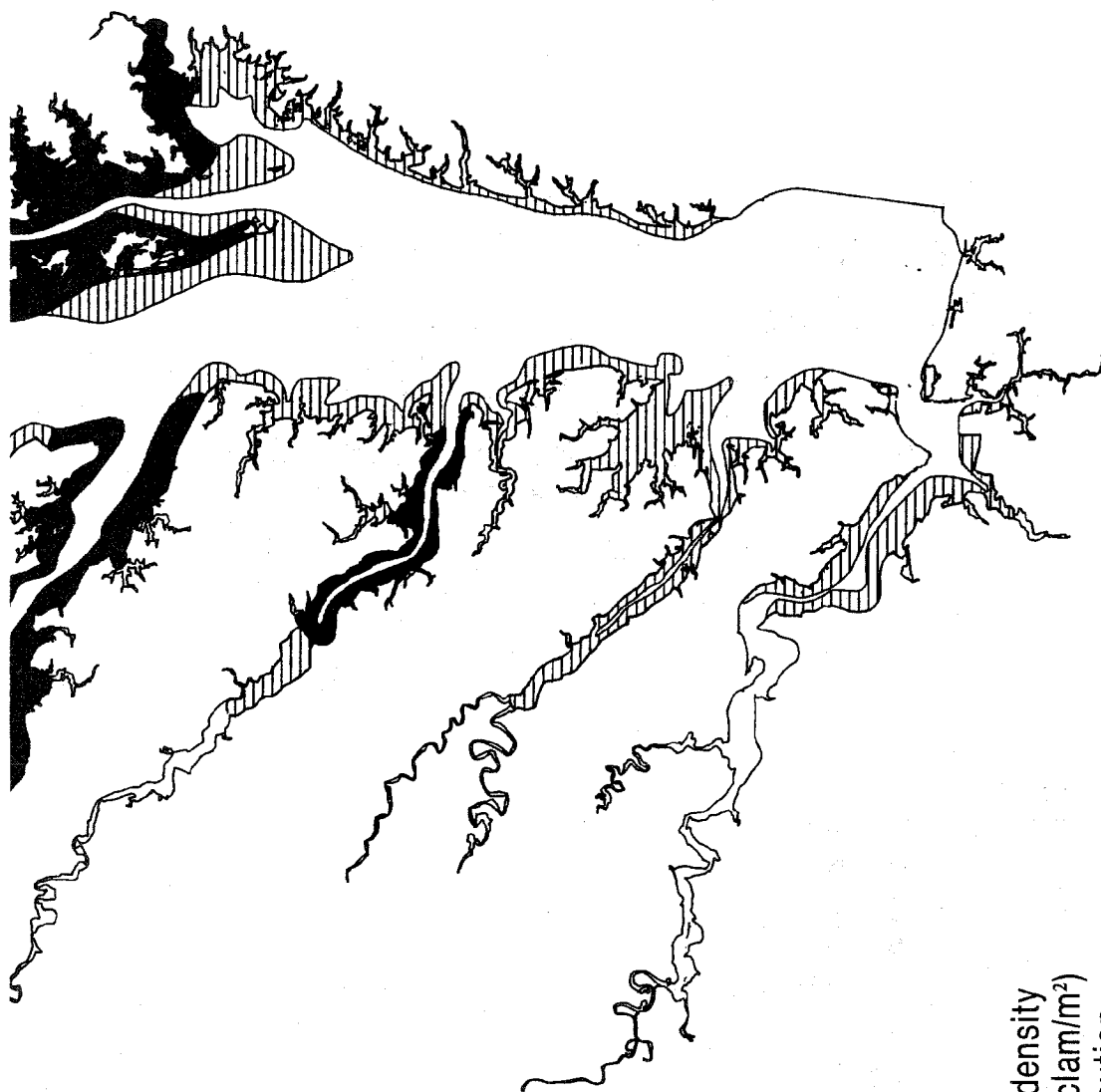
MAP 9





SOFT SHELL CLAM

Mya arenaria

Habitat Distribution
in the Chesapeake Bay

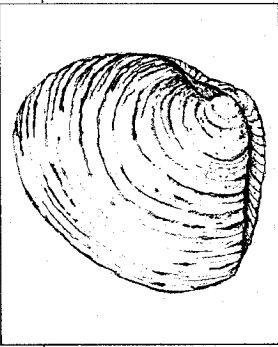


 High density
 $\geq 1 \text{ clam/m}^2$
 distribution

 Low density
 $< 1 \text{ clam/m}^2$
 distribution

SOURCES: New map by P. Baker, based
 on salinity, depth, and sediment habitat
 requirements, and literature reports of
 actual distribution.

Scale—1:1,069,000

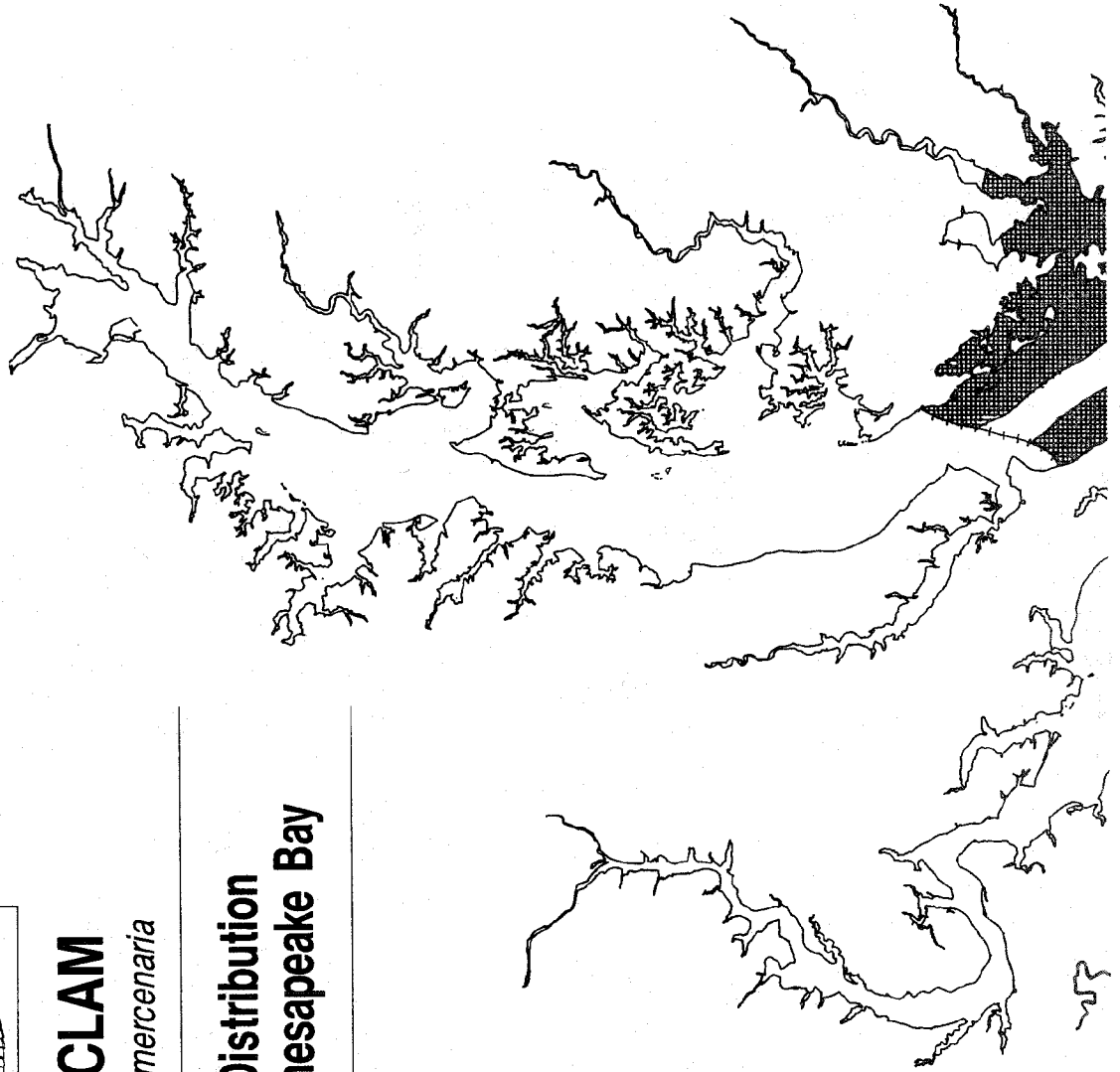
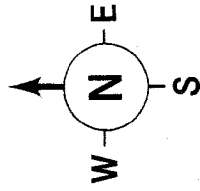


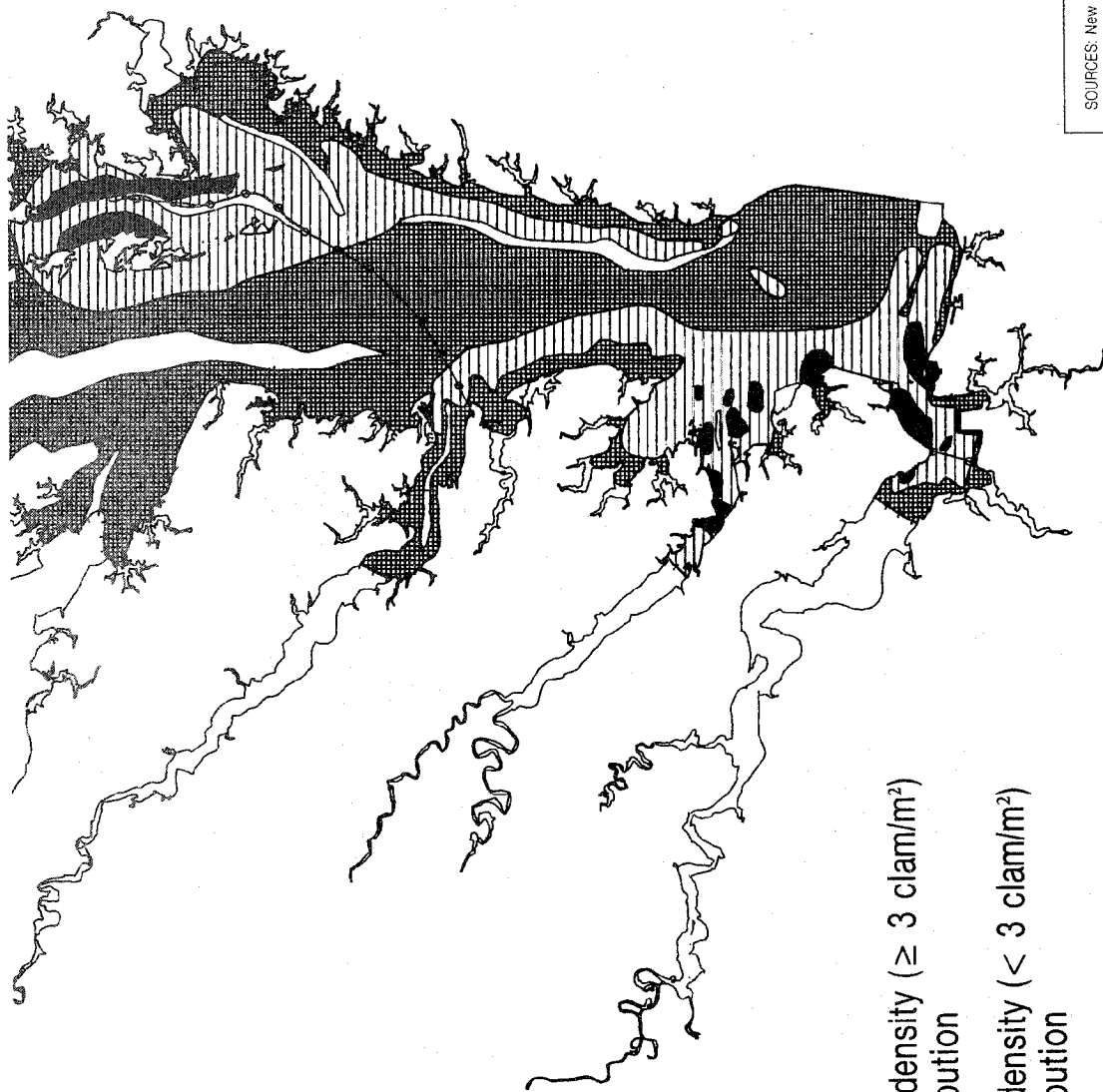
HARD CLAM

Mercenaria mercenaria

Habitat Distribution in the Chesapeake Bay

MAP 10





High density (≥ 3 clam/m²)
distribution



Low density (< 3 clam/m²)
distribution



Potential habitat



Adult salinity minimum-12 ppt.



Larval salinity minimum-15 ppt.



SOURCES: New map by C. Roegner,
based on salinity (> 12 ‰ summer
bottom average), depth (< 50 ft), and
sediment (sand-shell $>$ sand $>$ sand-
mud $>$ mud) habitat requirements, and
literature reports of actual distribution.

Scale—1:1,069,000

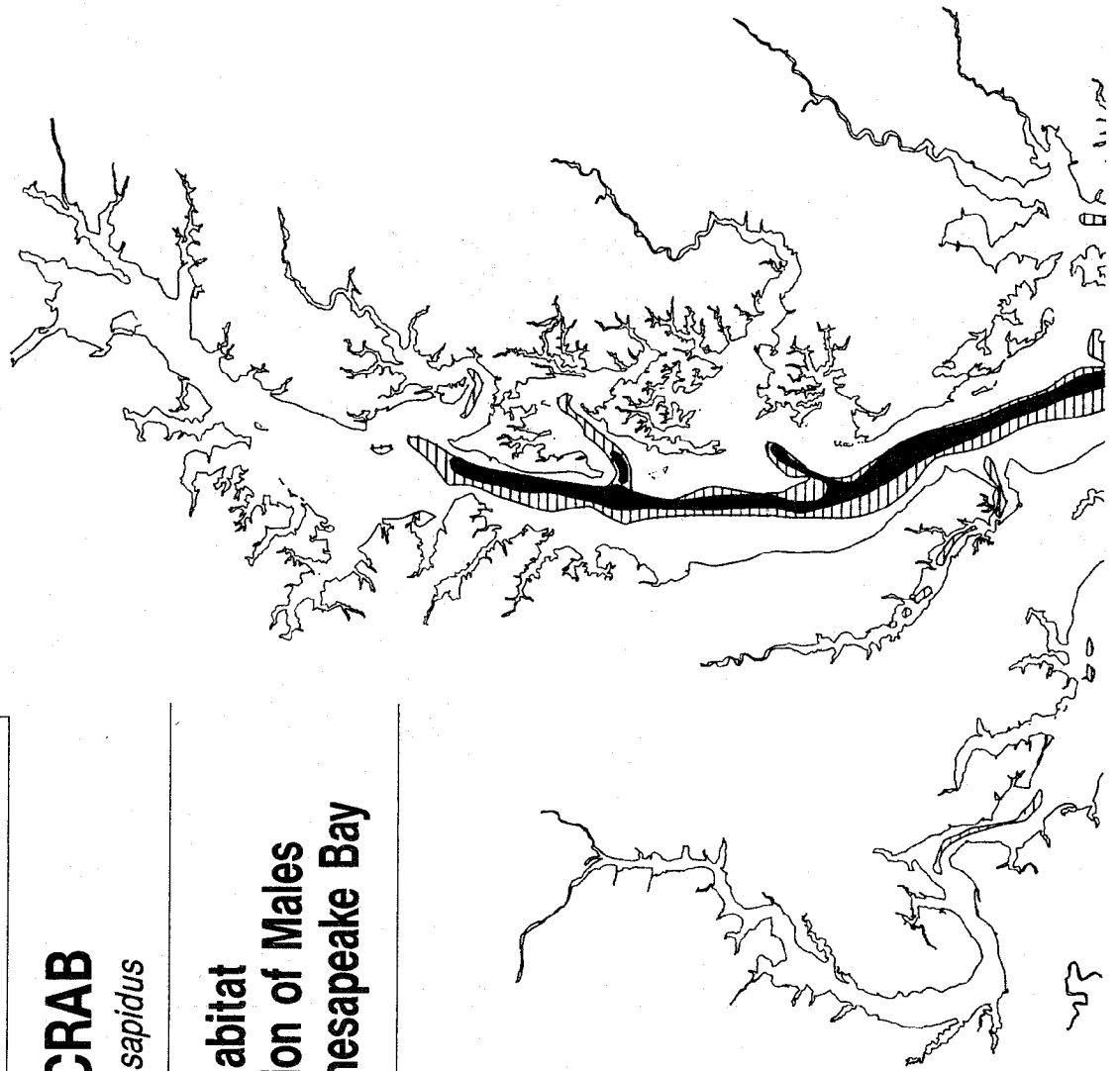
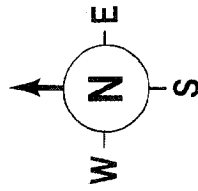


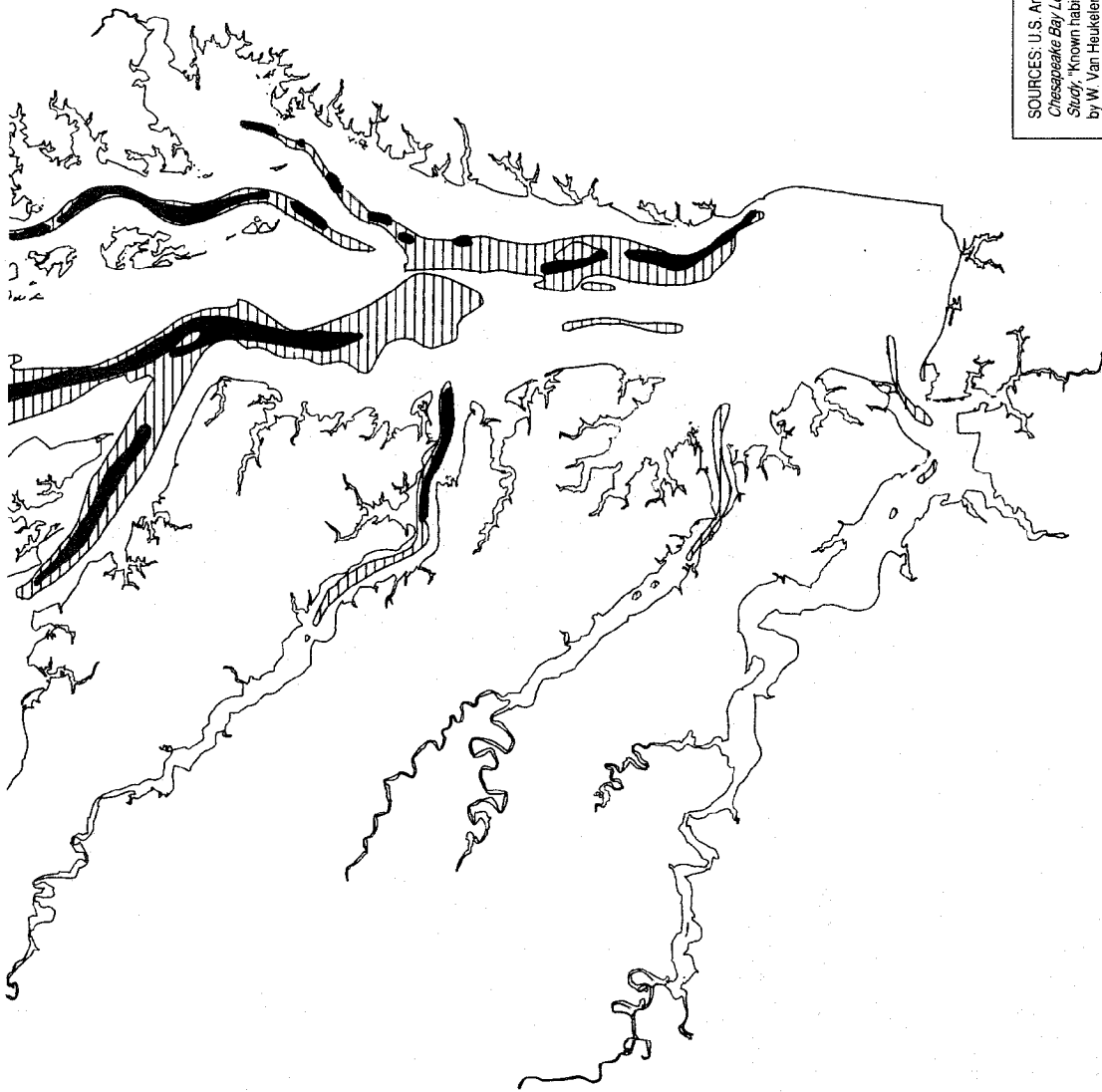
BLUE CRAB

Callinectes sapidus

Winter Habitat
Distribution of Males
in the Chesapeake Bay

MAP 11

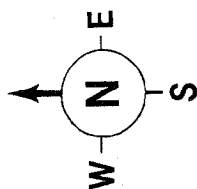




High density areas
Low density areas

SOURCES: U.S. Army Corps of Engineers, *Chesapeake Bay Low Freshwater Inflow Study*, "Known habitat" map, 1980, edited by W. Van Heukelem. Recent information collected by MDNR indicates a different distribution of winter habitat, not including the deep central mainstem of the Bay, but ranging more along the flanks of the mainstem and tributaries.

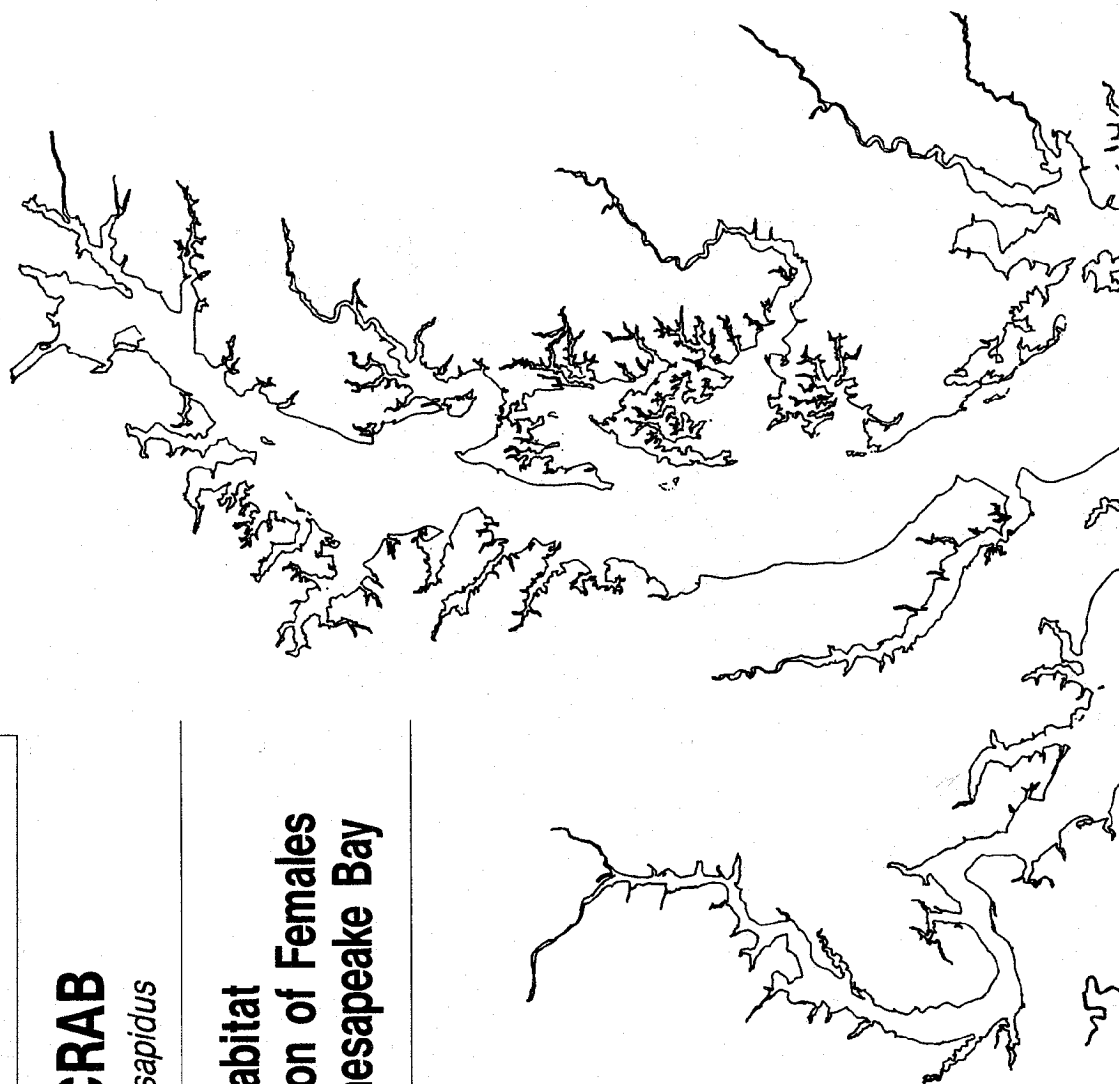
Scale—1:1,069,000

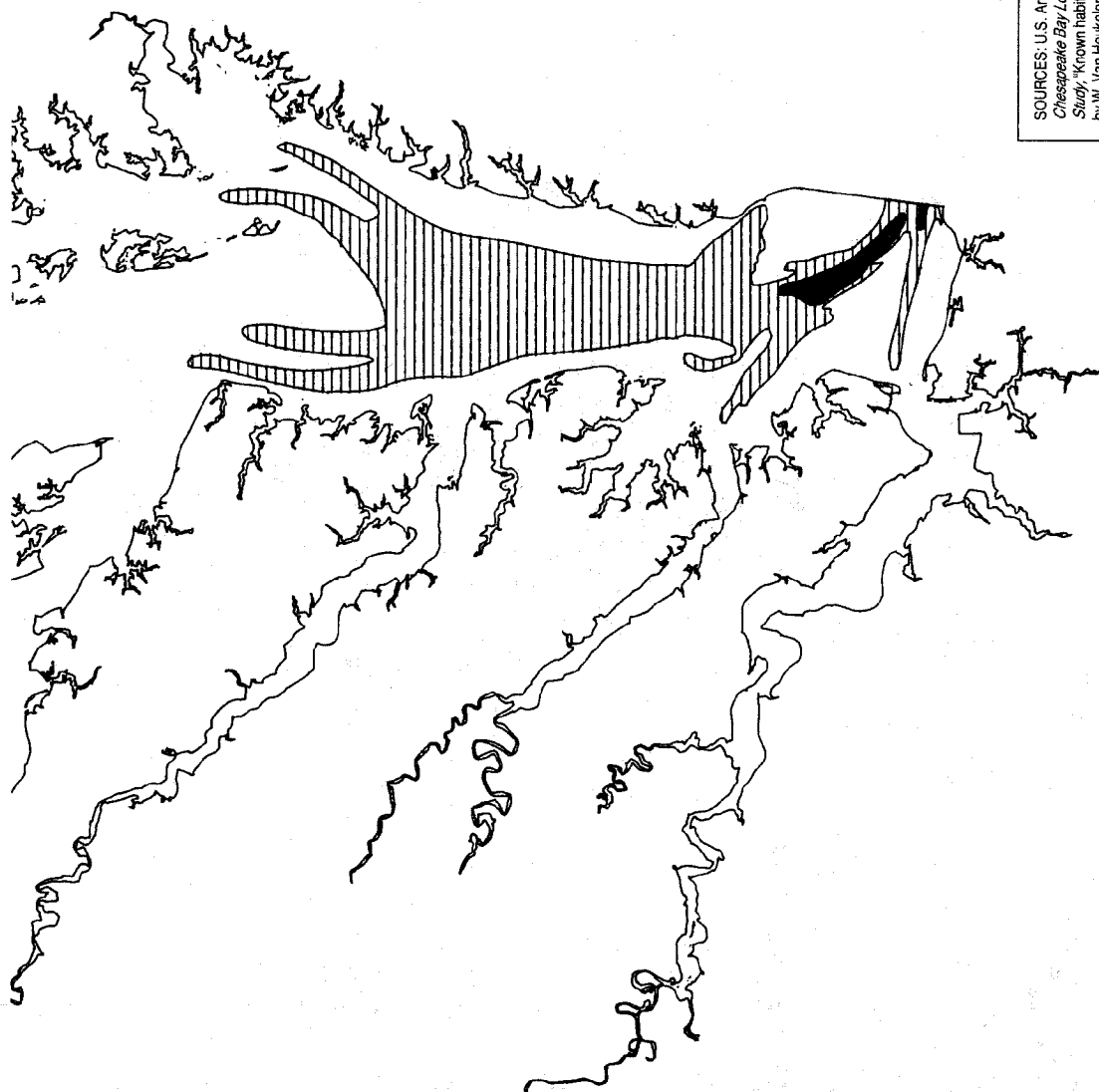




BLUE CRAB

Callinectes sapidus

Winter Habitat
Distribution of Females
in the Chesapeake Bay

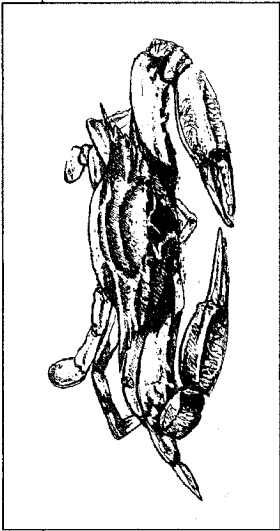




 High density areas
 Low density areas

SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
 Study*, "Known habitat" map, 1980, edited
 by W. Van Heukelem. Recent information
 collected by MDNR indicates a different
 distribution of winter habitat, not including
 the deep central mainstem of the Bay, but
 ranging more along the flanks of the
 mainstem and tributaries.

Scale—1:1,069,000

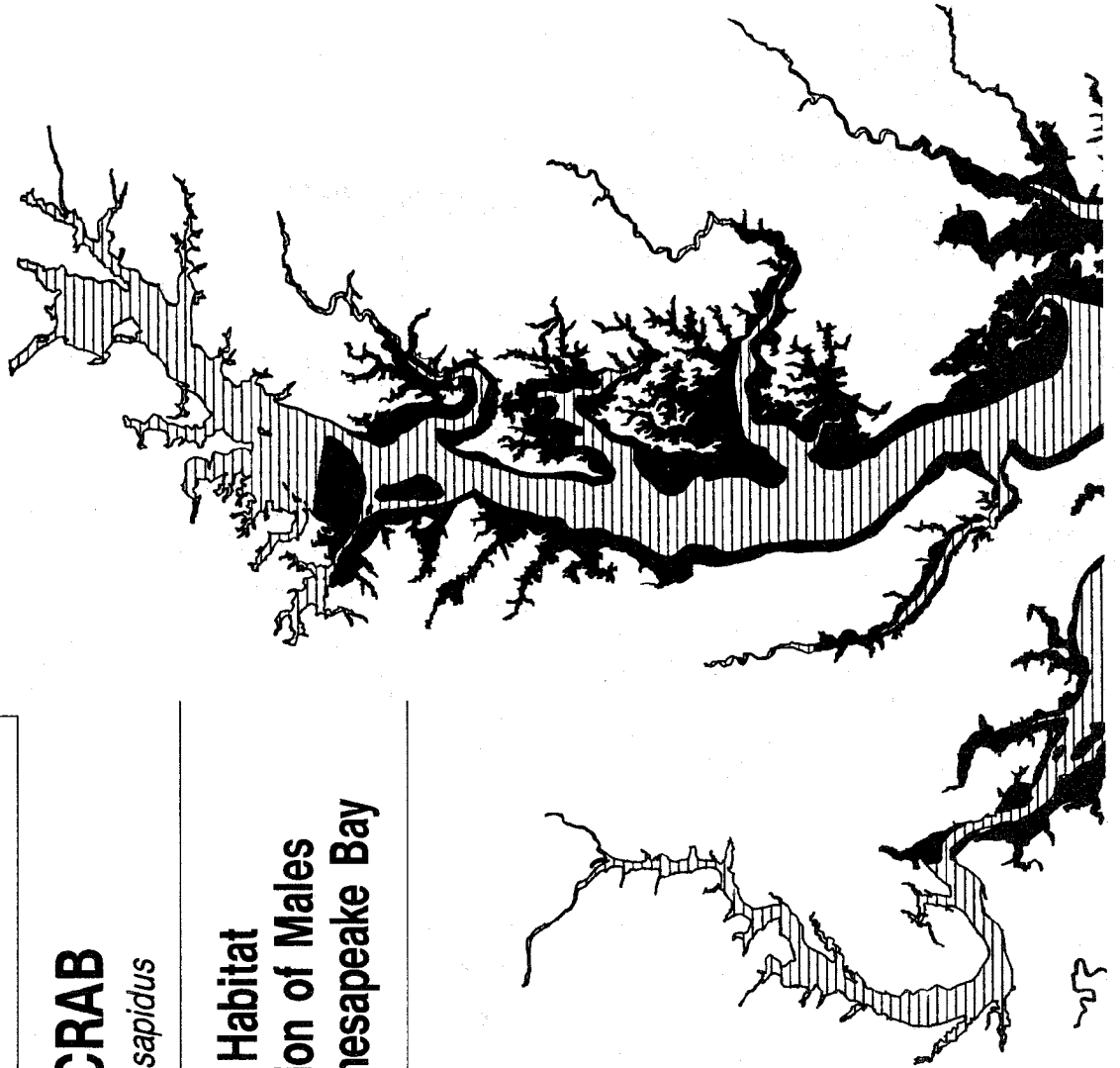
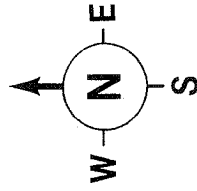


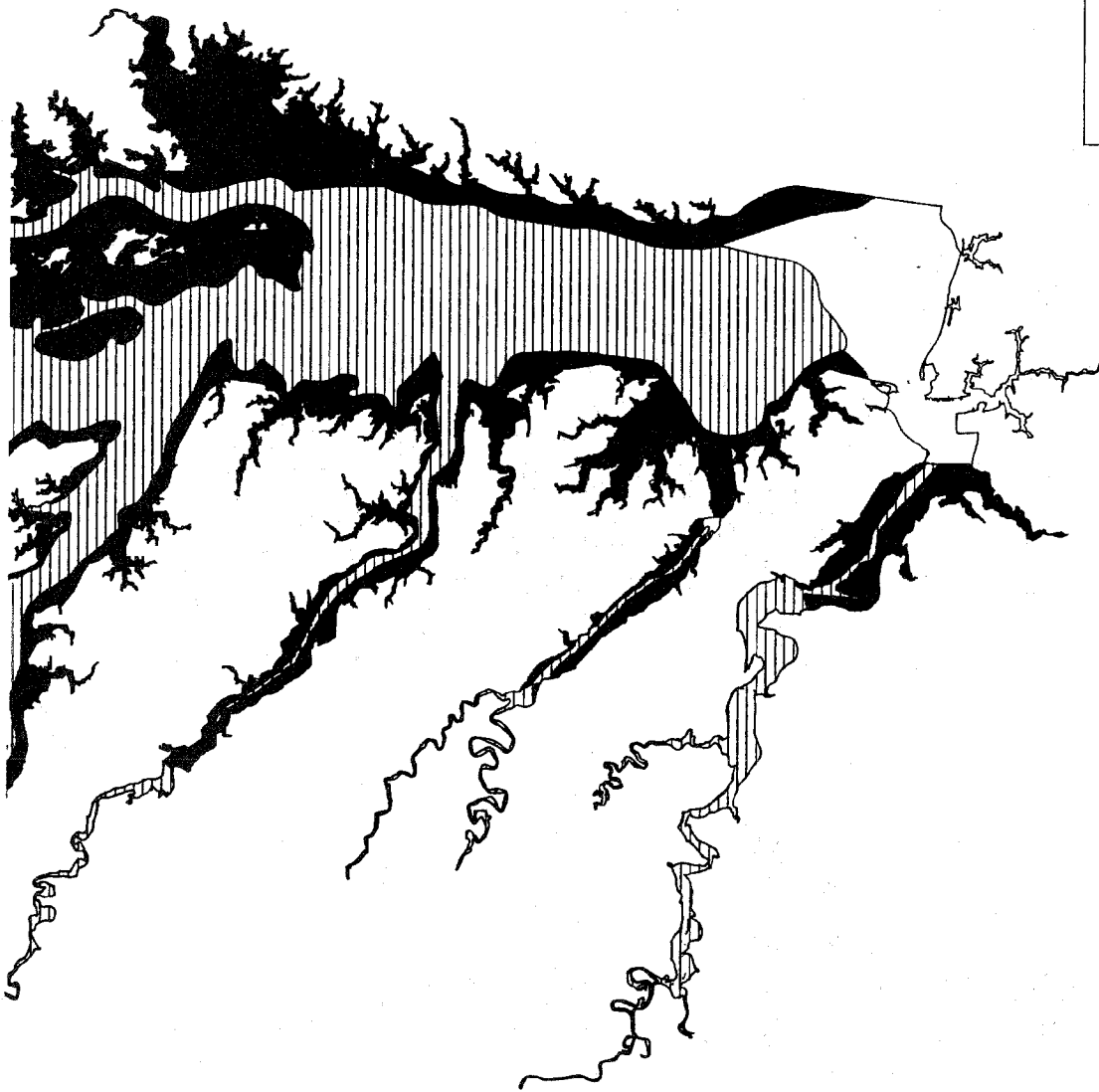
BLUE CRAB

Callinectes sapidus

Summer Habitat
Distribution of Males
in the Chesapeake Bay

MAP 13

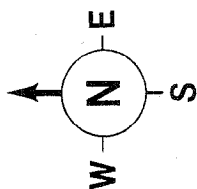




SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
Study*, known habitat map, 1980,
edited by W. Van Heukelem based on
more recent information.

High density areas
Low density areas

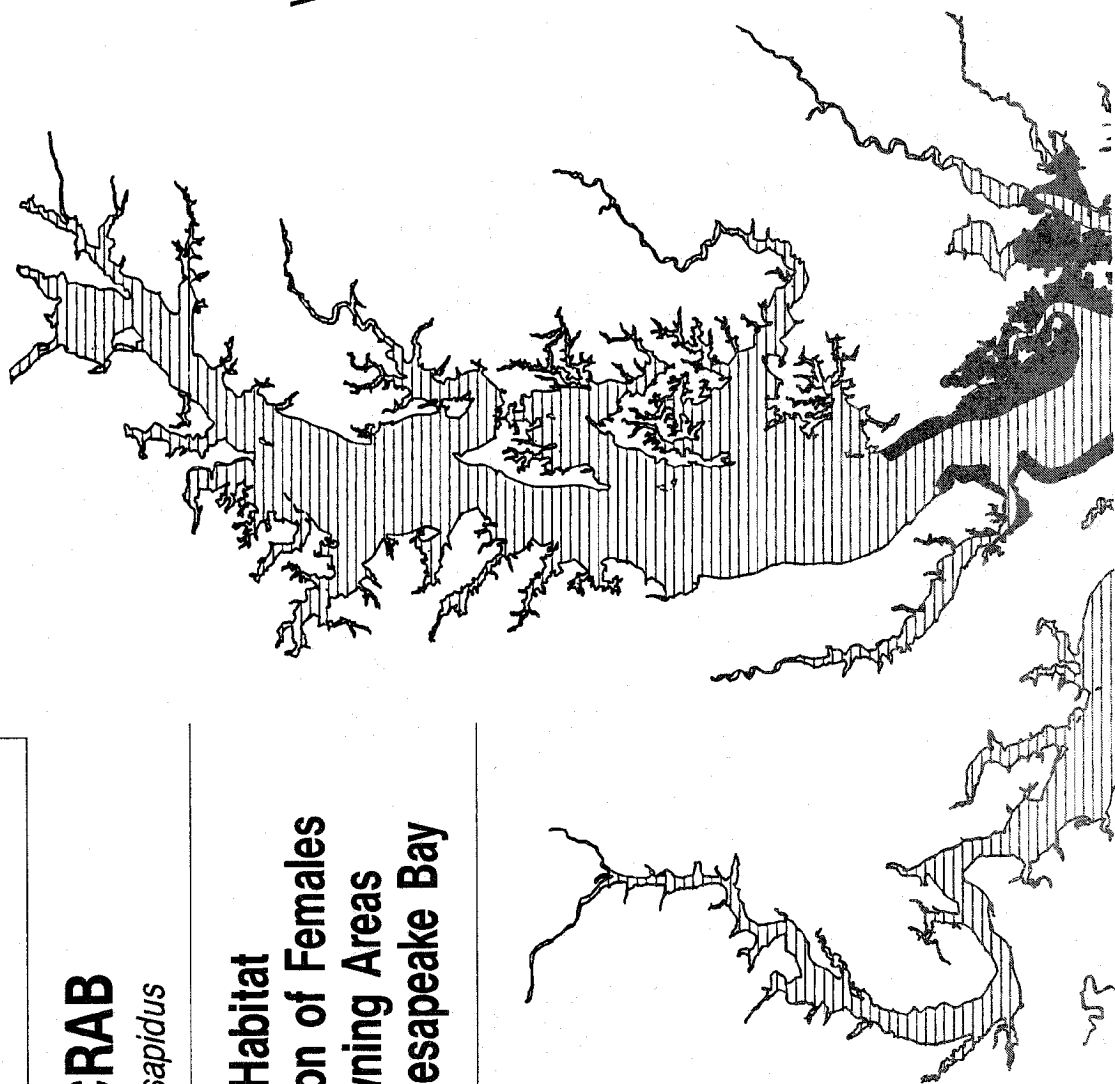
Scale—1:1,069,000

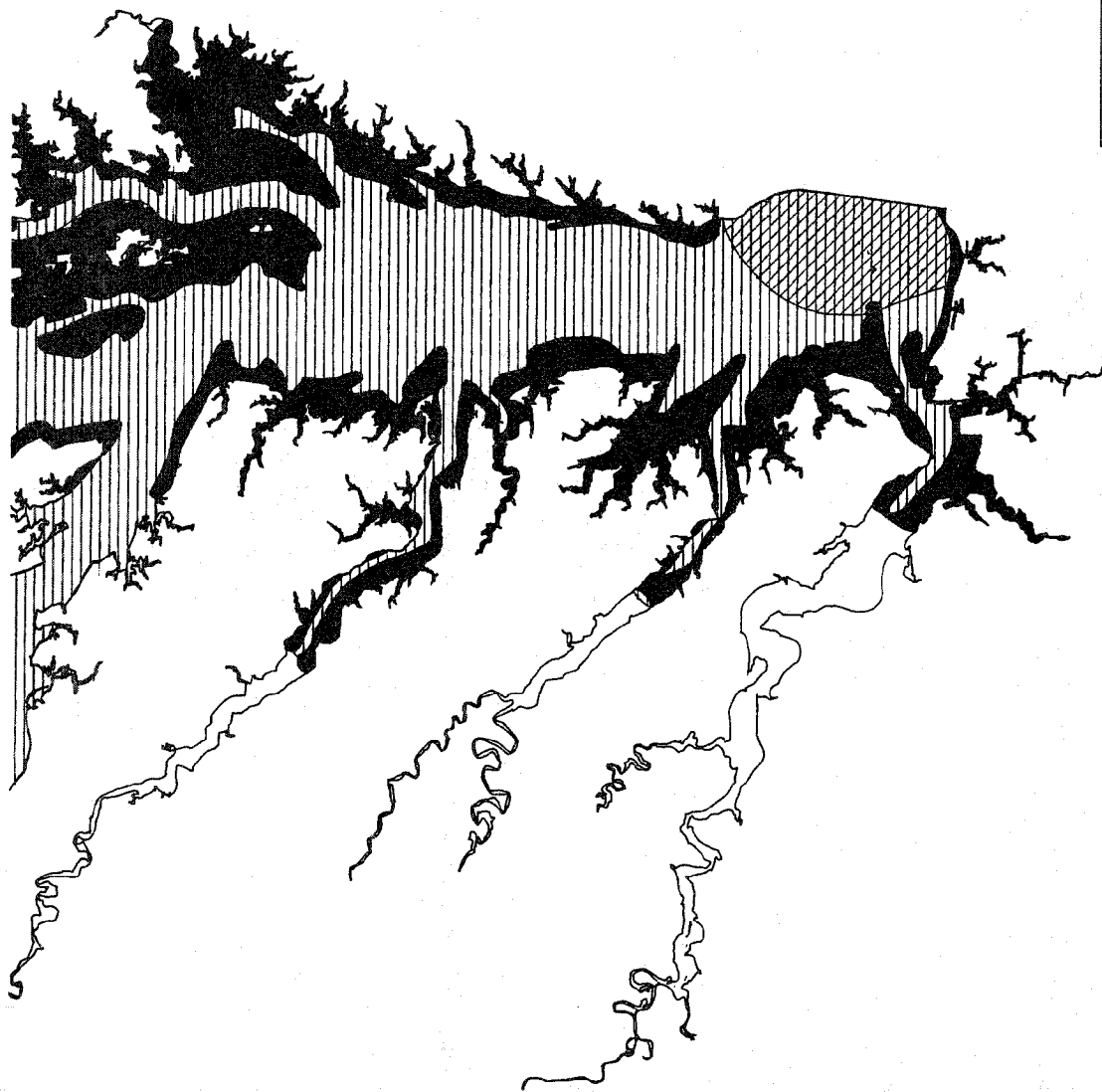


BLUE CRAB

Callinectes sapidus

Summer Habitat
Distribution of Females
and Spawning Areas
in the Chesapeake Bay

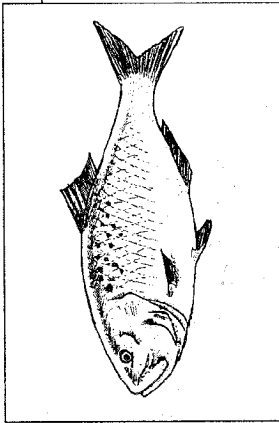




- High density areas
- Low density areas
- Spawning areas

SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
 Study*, "Known habitat" map, 1980,
 edited by W. Van Haukelern based on
 more recent information.

Scale — 1:1,069,000

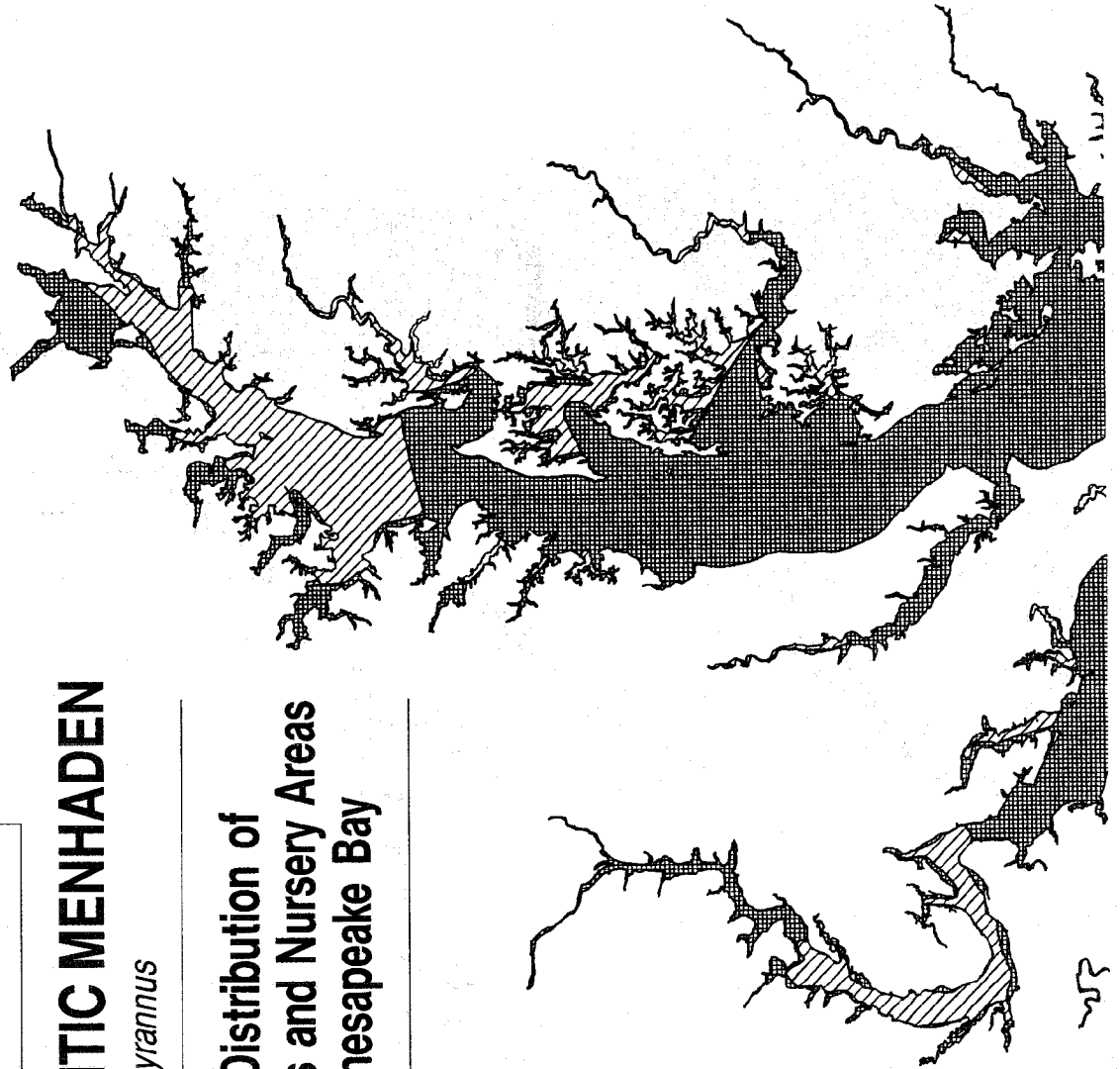


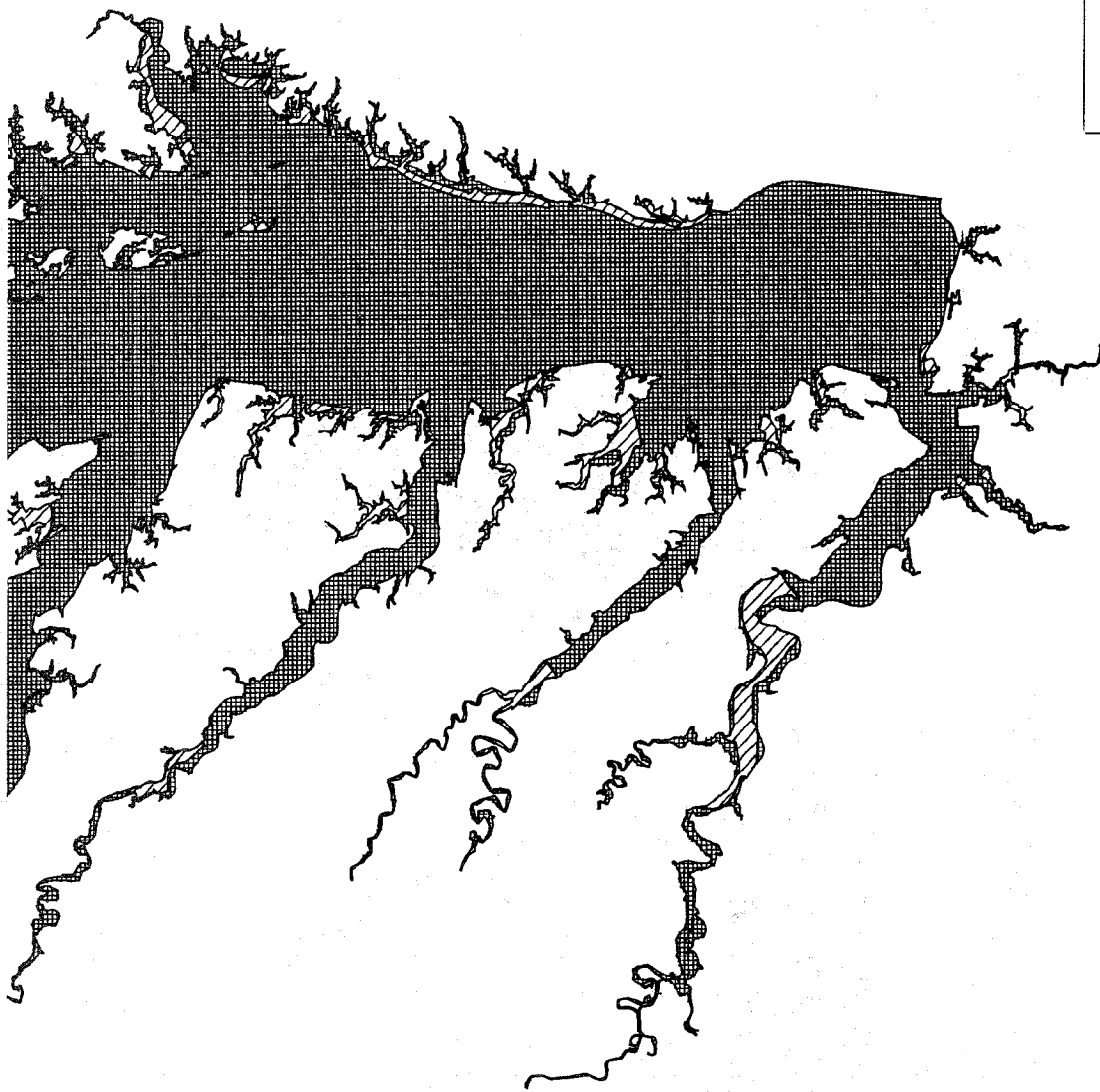
MAP 15

ATLANTIC MENHADEN



Brevoortia tyrannus

Habitat Distribution of
Juveniles and Nursery Areas
in the Chesapeake Bay

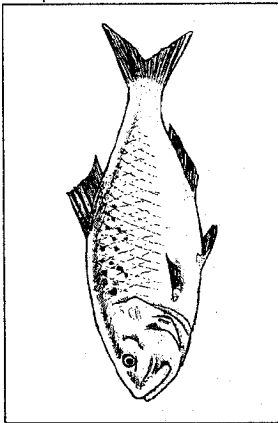




SOURCES: U.S. Army Corps of Engineers,
Chesapeake Bay Low Freshwater Inflow
Study, "Known & potential habitat" map,
1960; and A. J. Lippson, *The Chesapeake
Bay in Maryland*, 1973.

 Nursery areas
 General distribution
 (Juveniles)

Scale—1:1,069,000

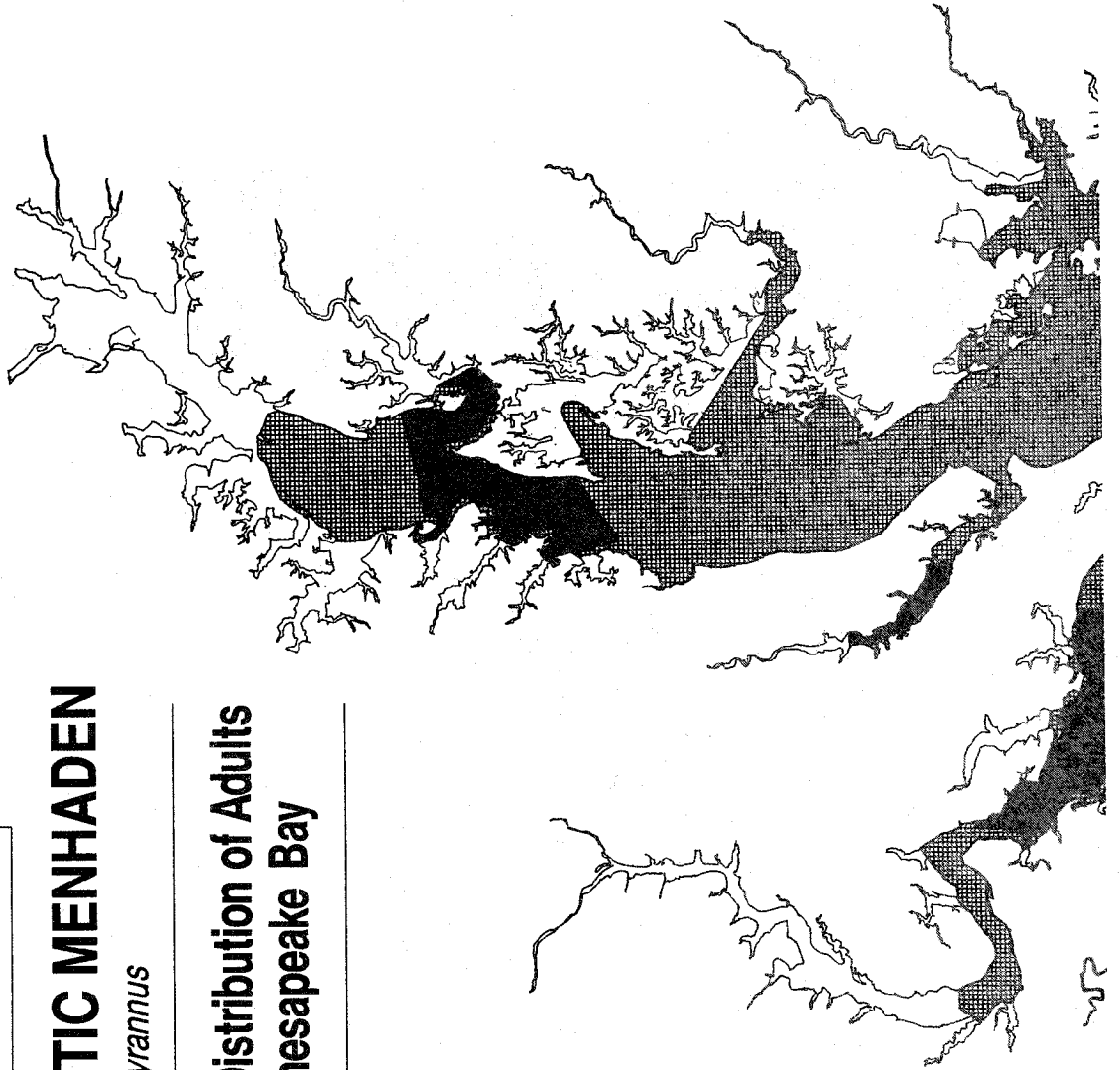
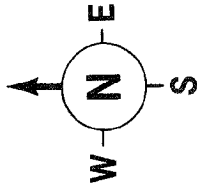


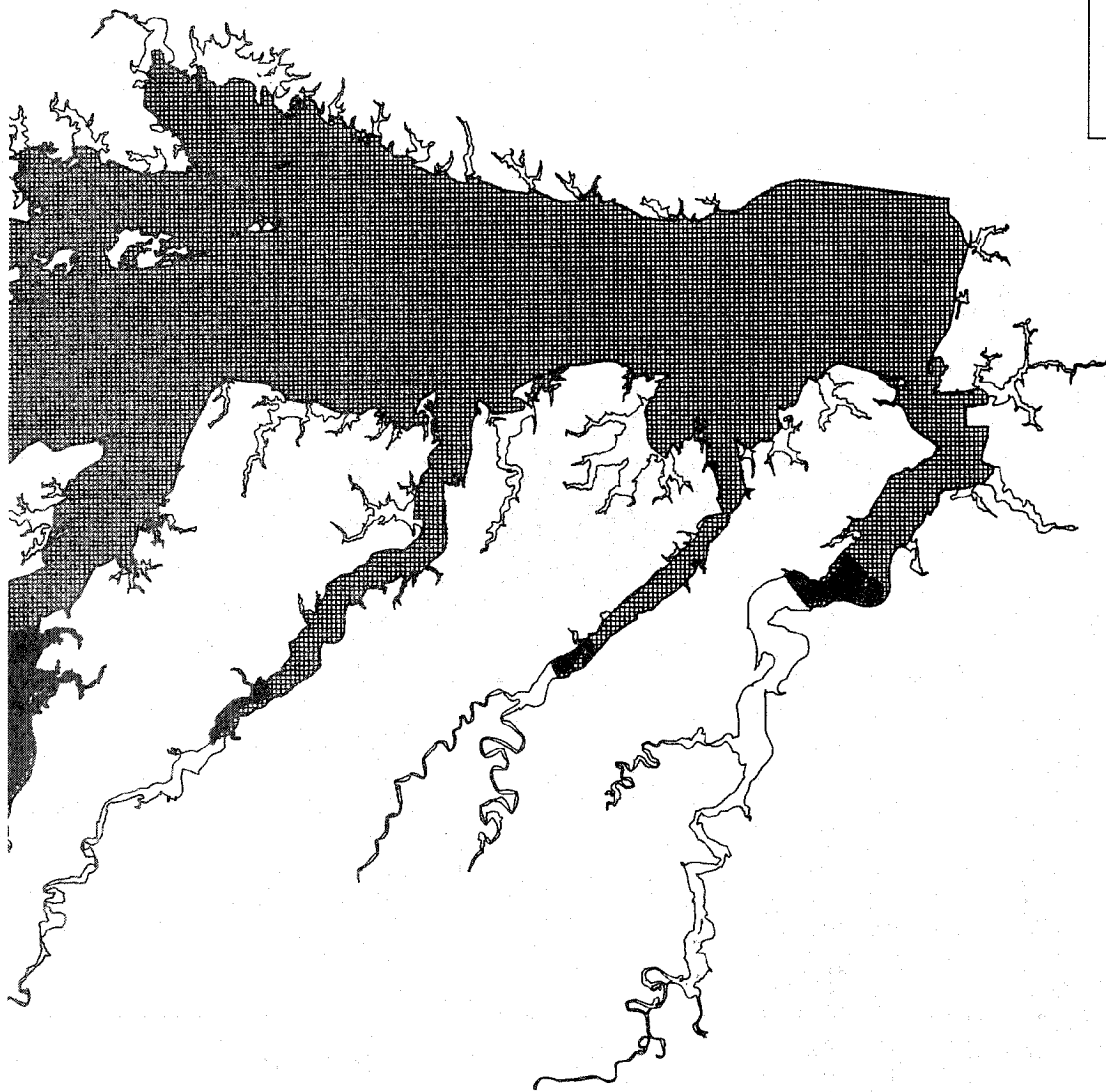
MAP 16

ATLANTIC MENHADEN

Brevoortia tyrannus

Habitat Distribution of Adults
in the Chesapeake Bay

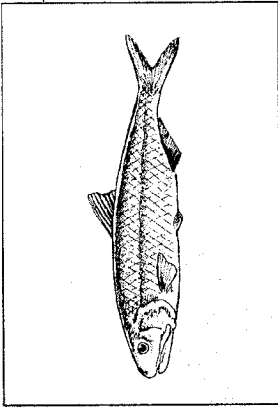




■ Concentration areas
▨ General distribution

SOURCES: U.S. Army Corps of Engineers, *Chesapeake Bay Low Freshwater Inflow Study*, "Known & potential habitat" map, 1980; and A. J. Lippson, *The Chesapeake Bay in Maryland*, 1973.

Scale—1:1,069,000

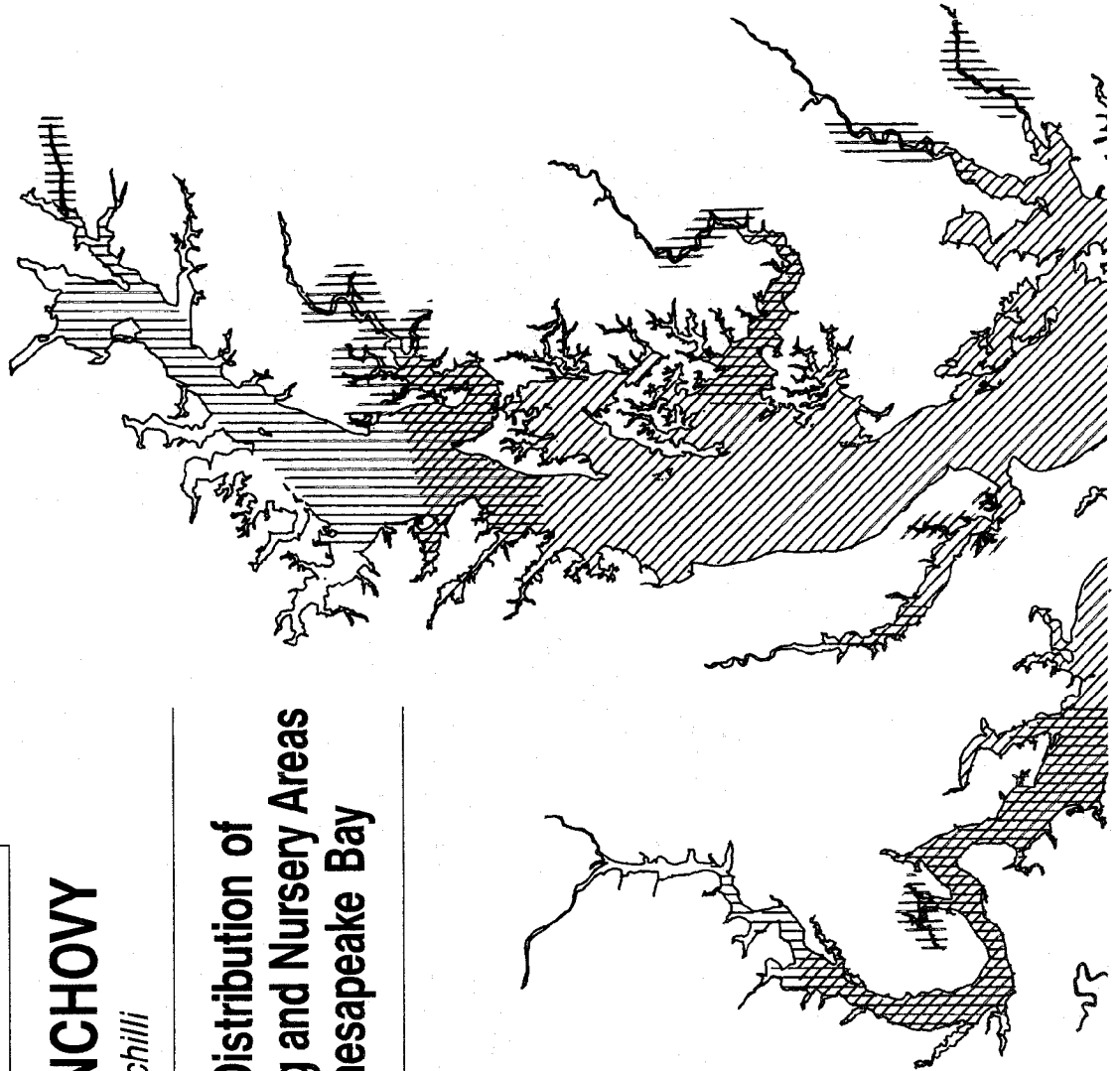


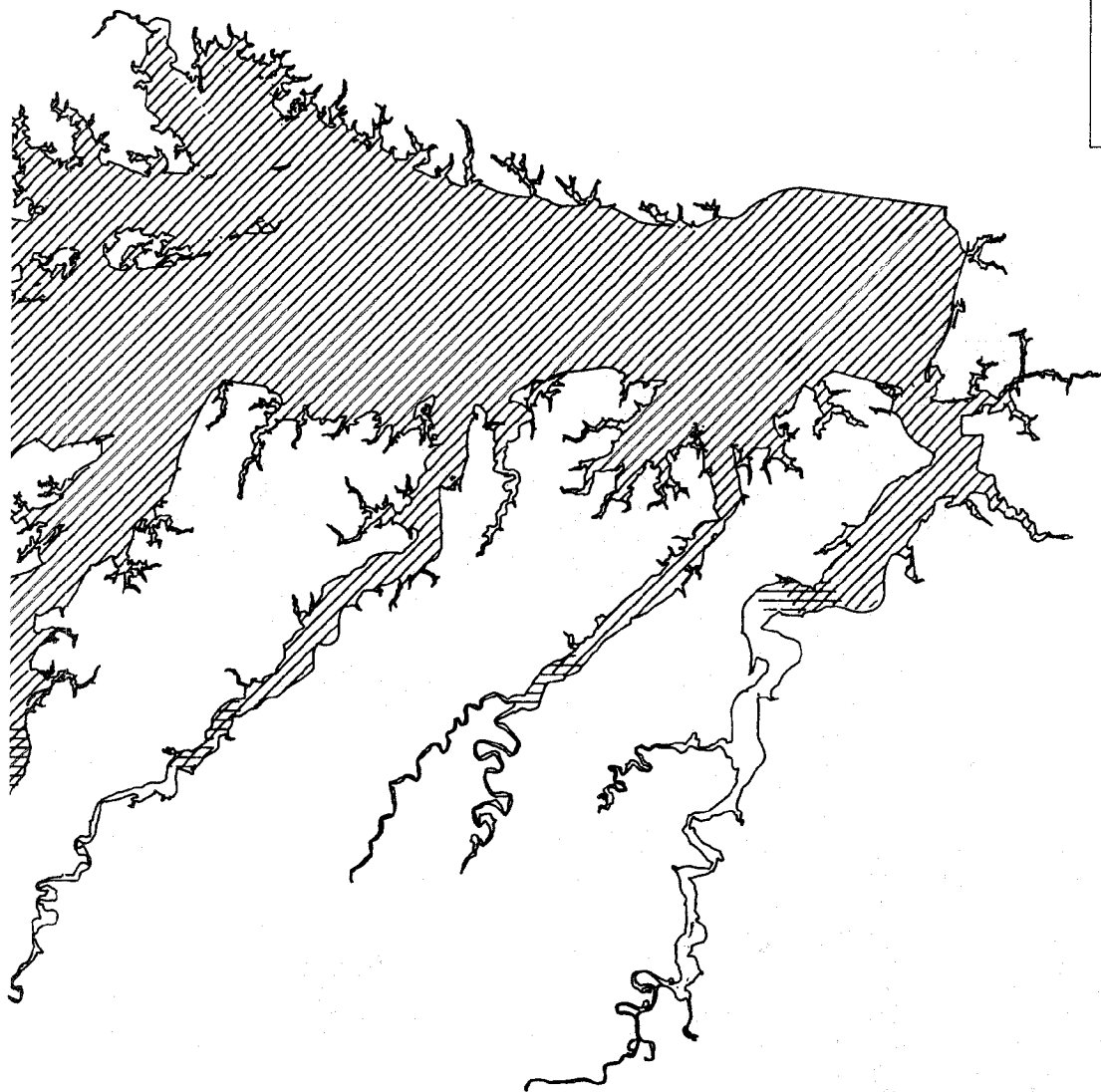
MAP 17

BAY ANCHOVY

Anchoa mitchilli

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay

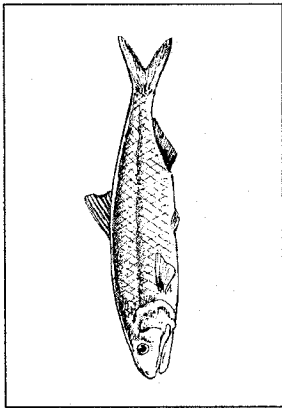




Spawning areas
Nursery areas

SOURCES: U.S. Army Corps of Engineers,
Chesapeake Bay Low Freshwater Inflow
Study, "Known & potential habitat"
map, 1980, edited by E. Houde based
on more recent information.

Scale—1:1,069,000

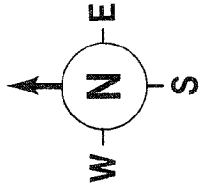
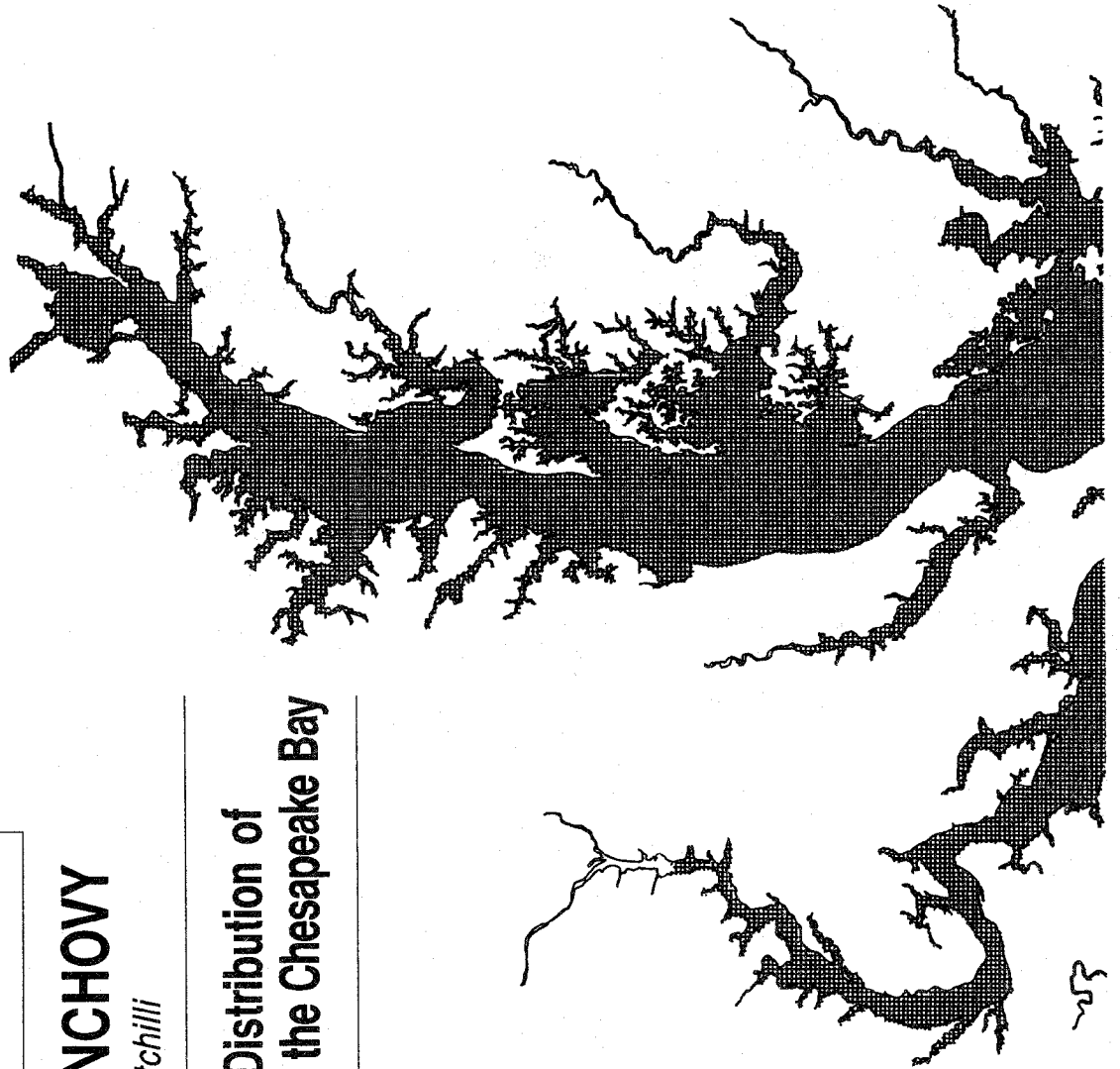


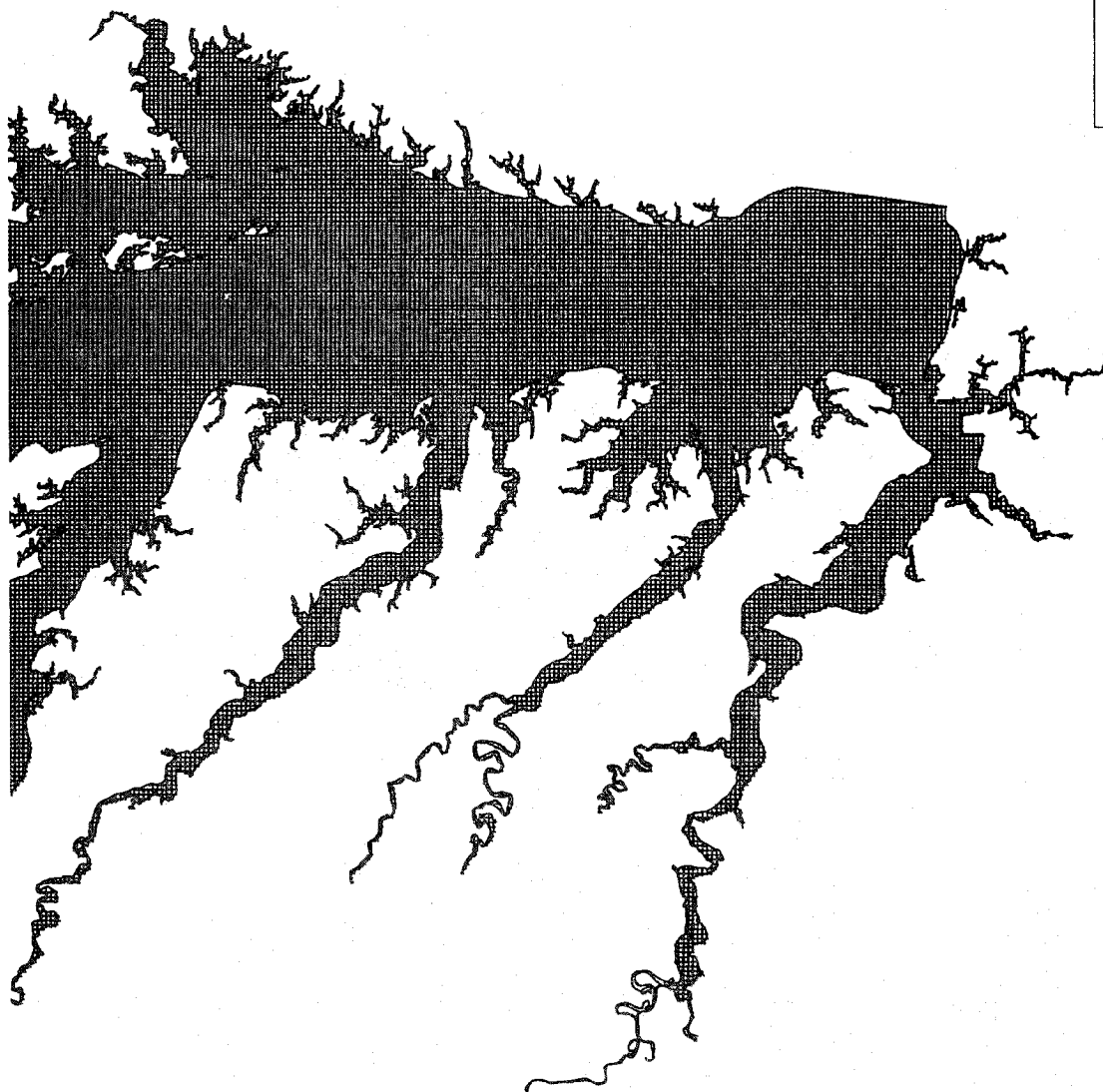
MAP 18

BAY ANCHOVY

Anchoa mitchilli

**Habitat Distribution of
Adults in the Chesapeake Bay**

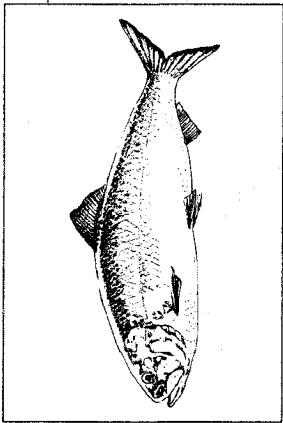




SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
Study*, "Known & potential habitat"
map, 1980, edited by E. Houde based
on more recent information.

■ Potential distribution

Scale—1:1,069,000

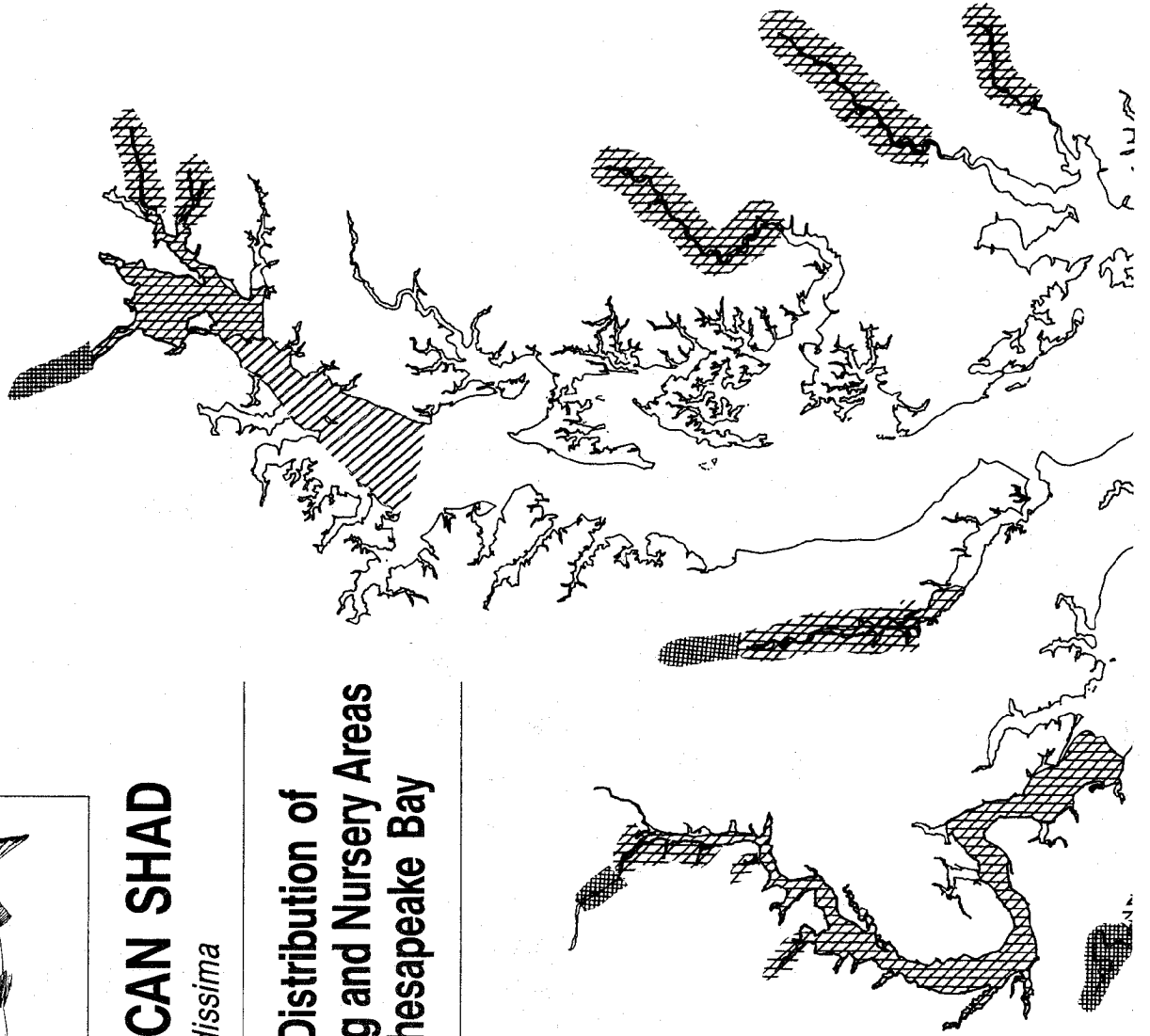
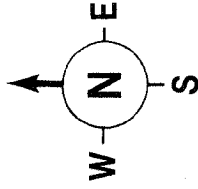


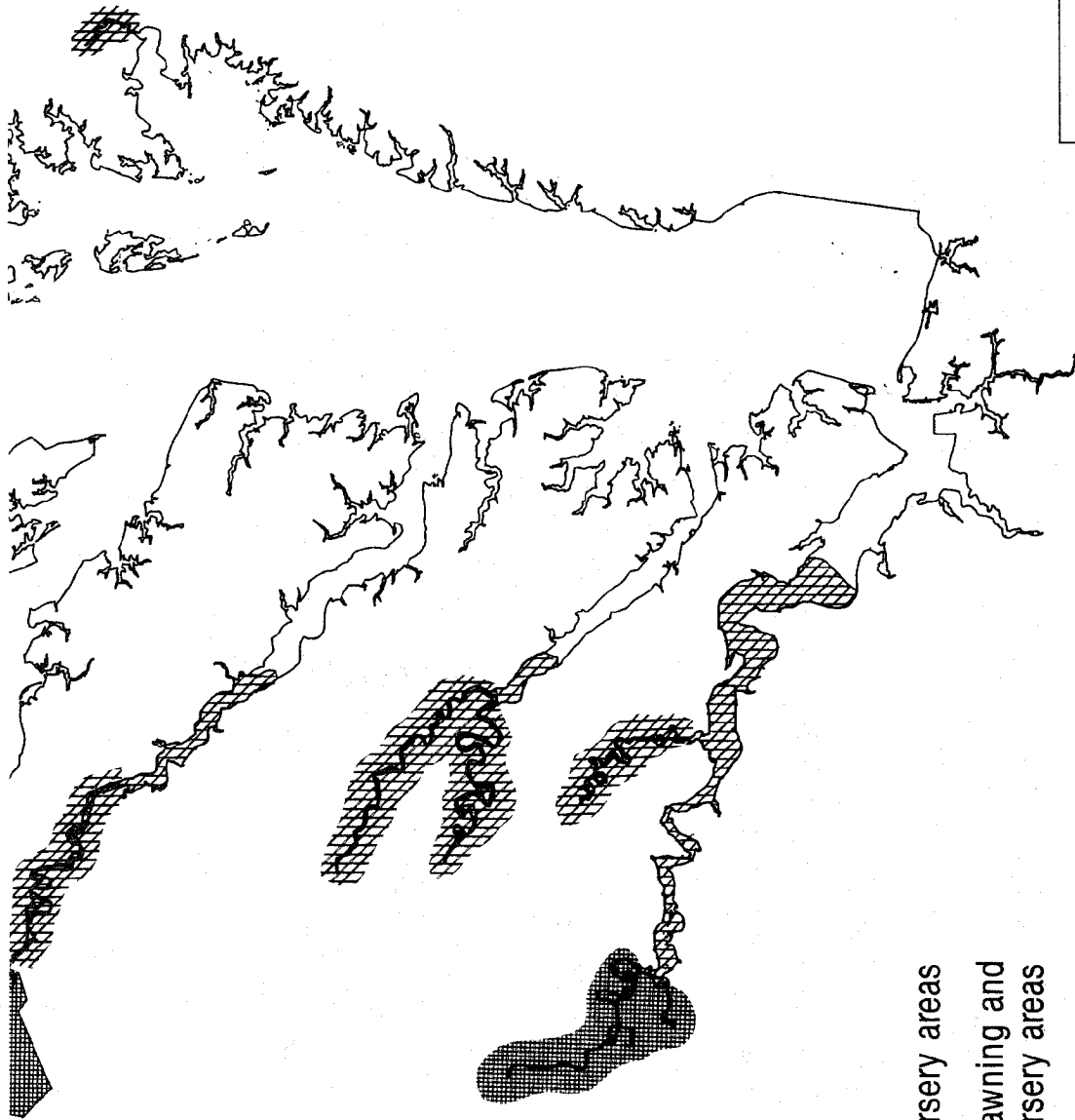
AMERICAN SHAD




Alosa sapidissima

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay

MAP 19

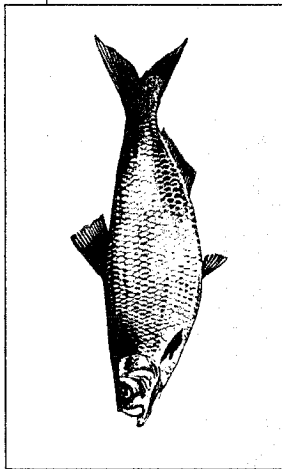




-  Nursery areas
-  Spawning and Nursery areas
-  Potential extended distribution if blockages are removed or bypassed

SOURCES: U.S. Army Corps of Engineers, Chesapeake Bay Low Freshwater Inflow Study, "Known & potential habitat" map, 1980, edited by R. Klauda based on more recent information.

Scale—1:1,069,000



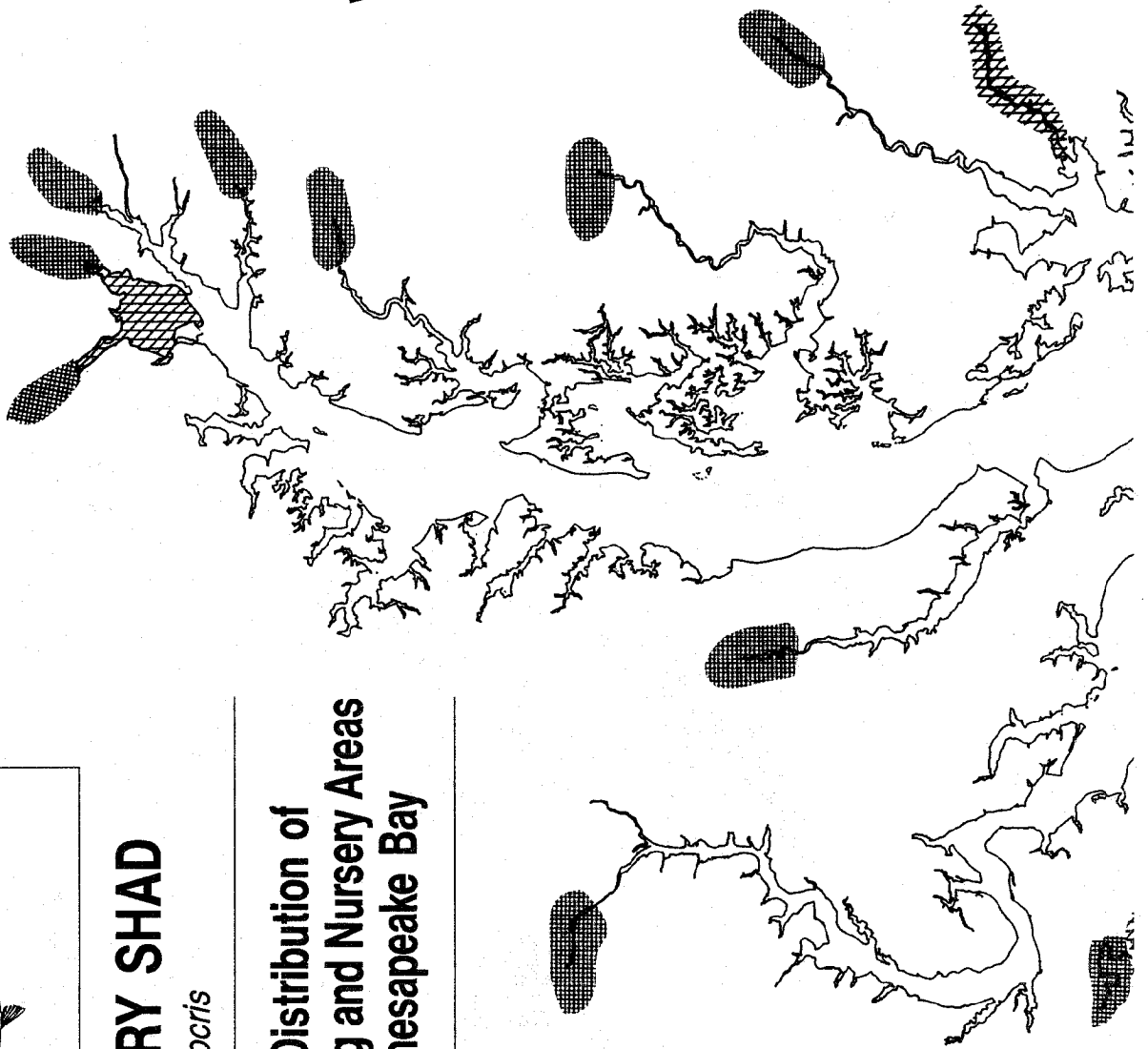
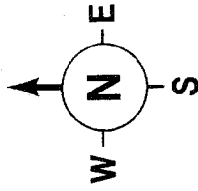
HICKORY SHAD

Alosa mediocris


Habitat Distribution of Spawning and Nursery Areas in the Chesapeake Bay


Drawings courtesy Duane Raver, Jr.

MAP 20



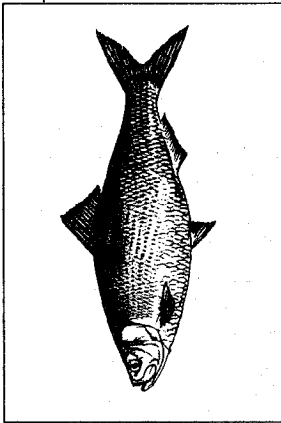


 Spawning and
Nursery areas

 Potential extended
distribution if
blockages are
removed or bypassed

SOURCES: U.S. Army Corps of Engineers,
 Chesapeake Bay Low Freshwater Inflow
 Study, "Known & potential habitat"
 map, 1980, edited by R. Klauca based
 on more recent information.

Scale—1:1,069,000



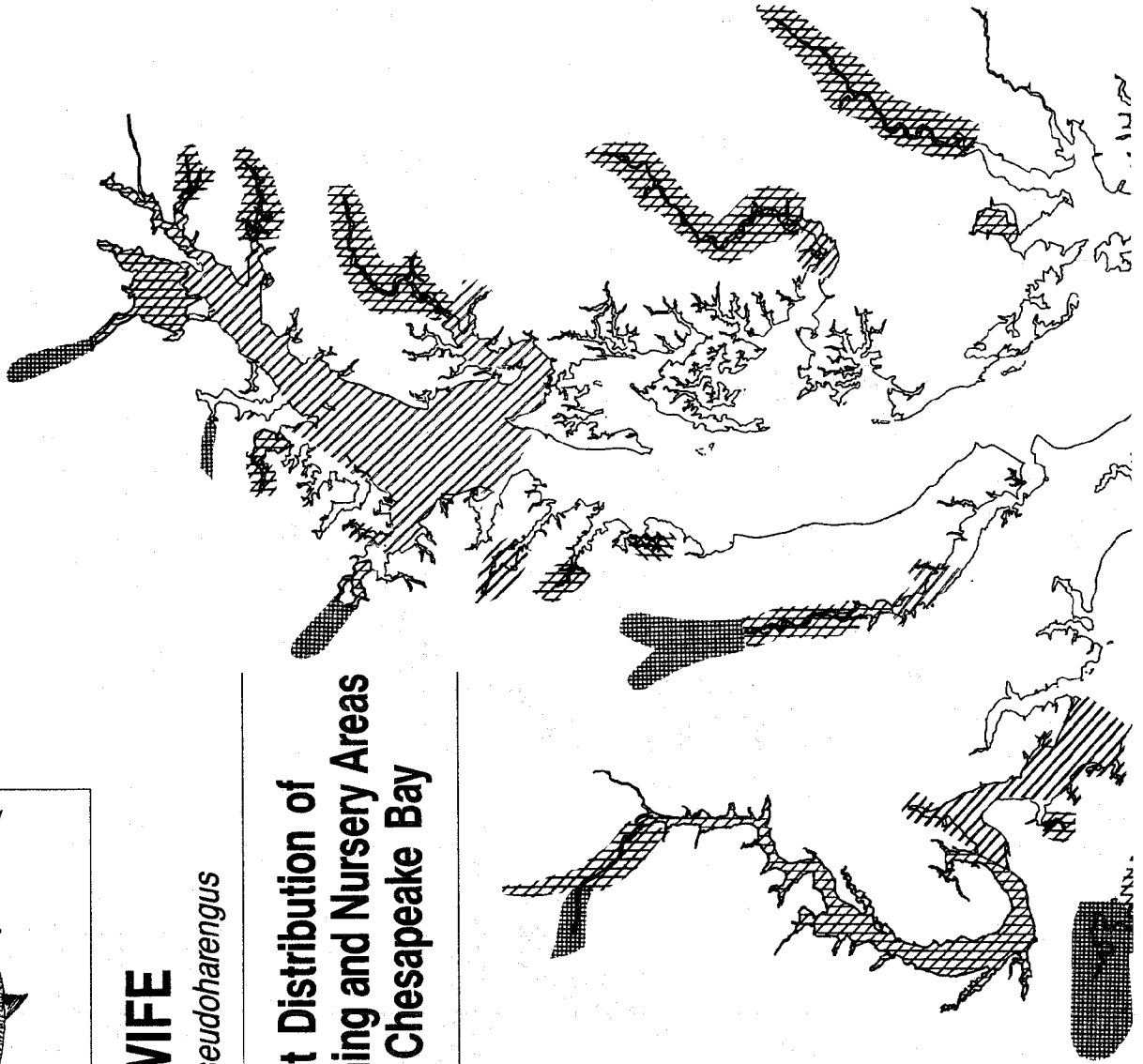
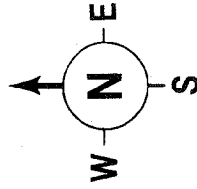
Drawings courtesy Duane Raver, Jr.

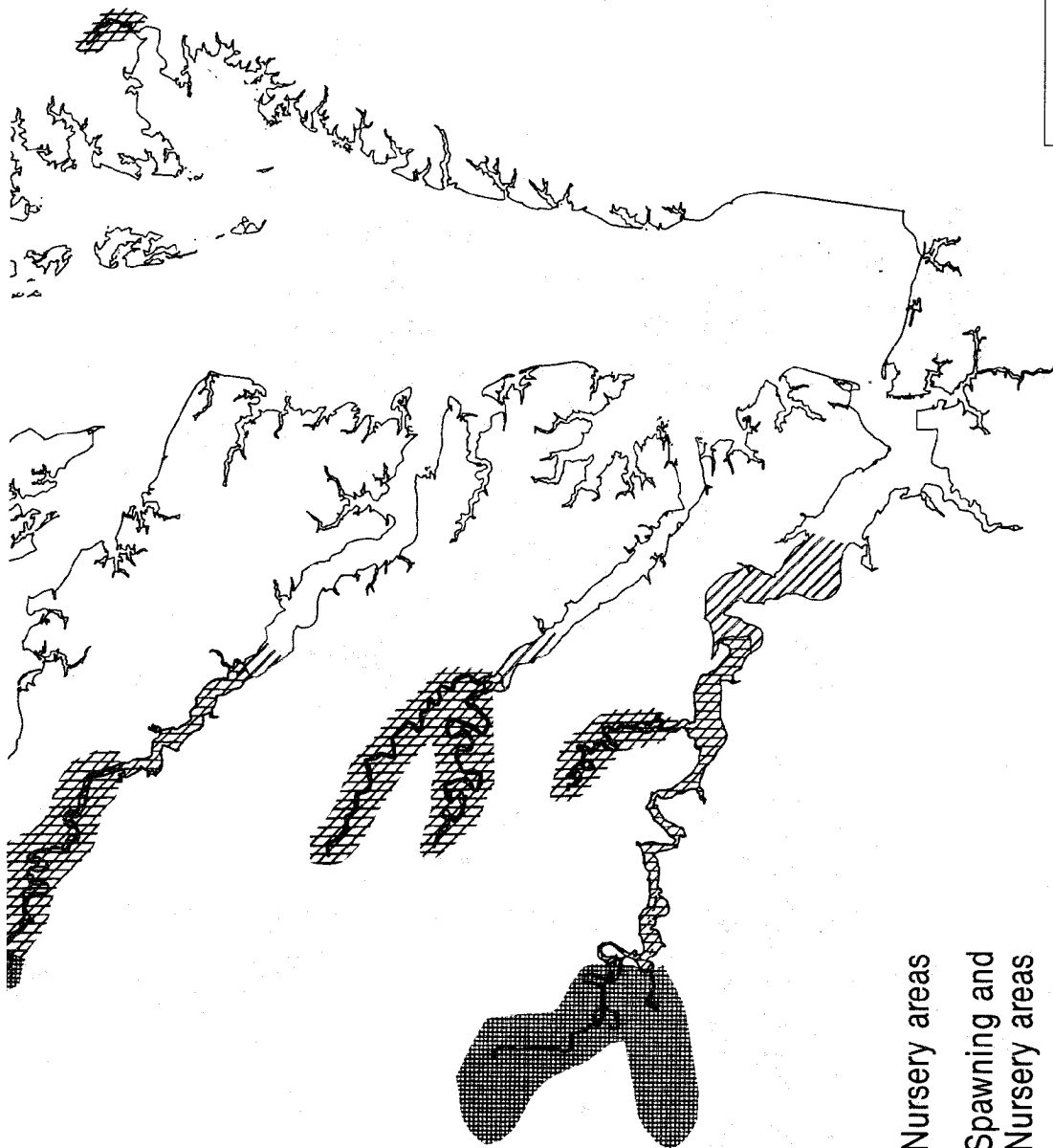
MAP 21

ALEWIFE

Alosa pseudoharengus

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay





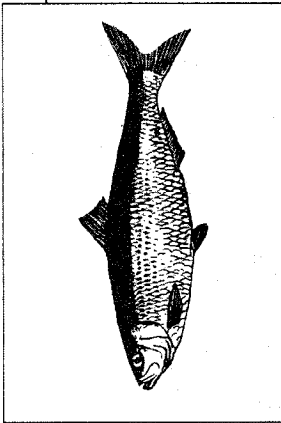
Nursery areas

Spawning and
Nursery areas

Potential extended
distribution if
blockages are
removed or bypassed

SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
Study*, "Known & potential habitat" map,
1980, edited by R. Klauda based on
more recent information.

Scale—1:1,069,000



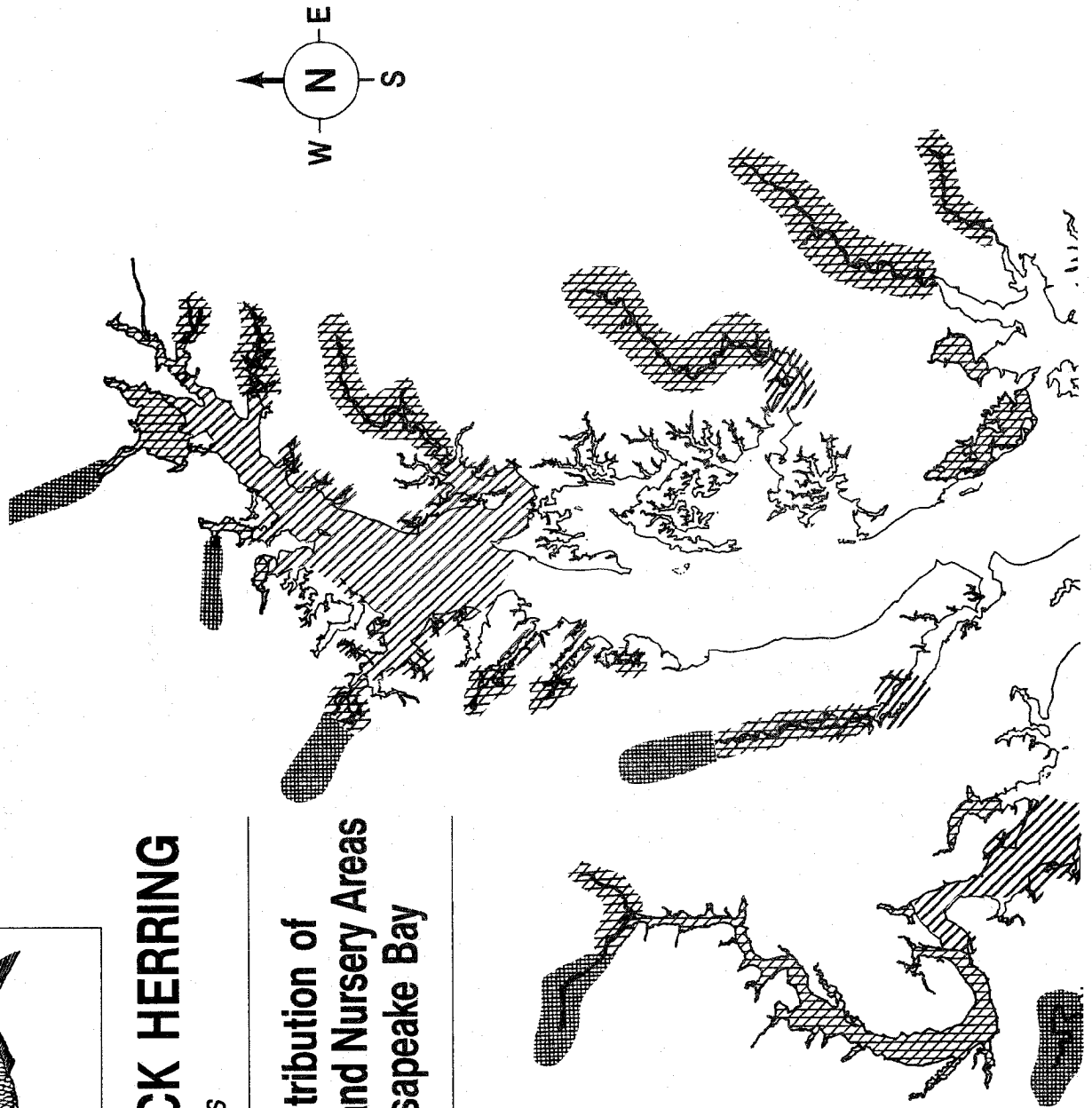
Drawings courtesy Duane Raver, Jr.

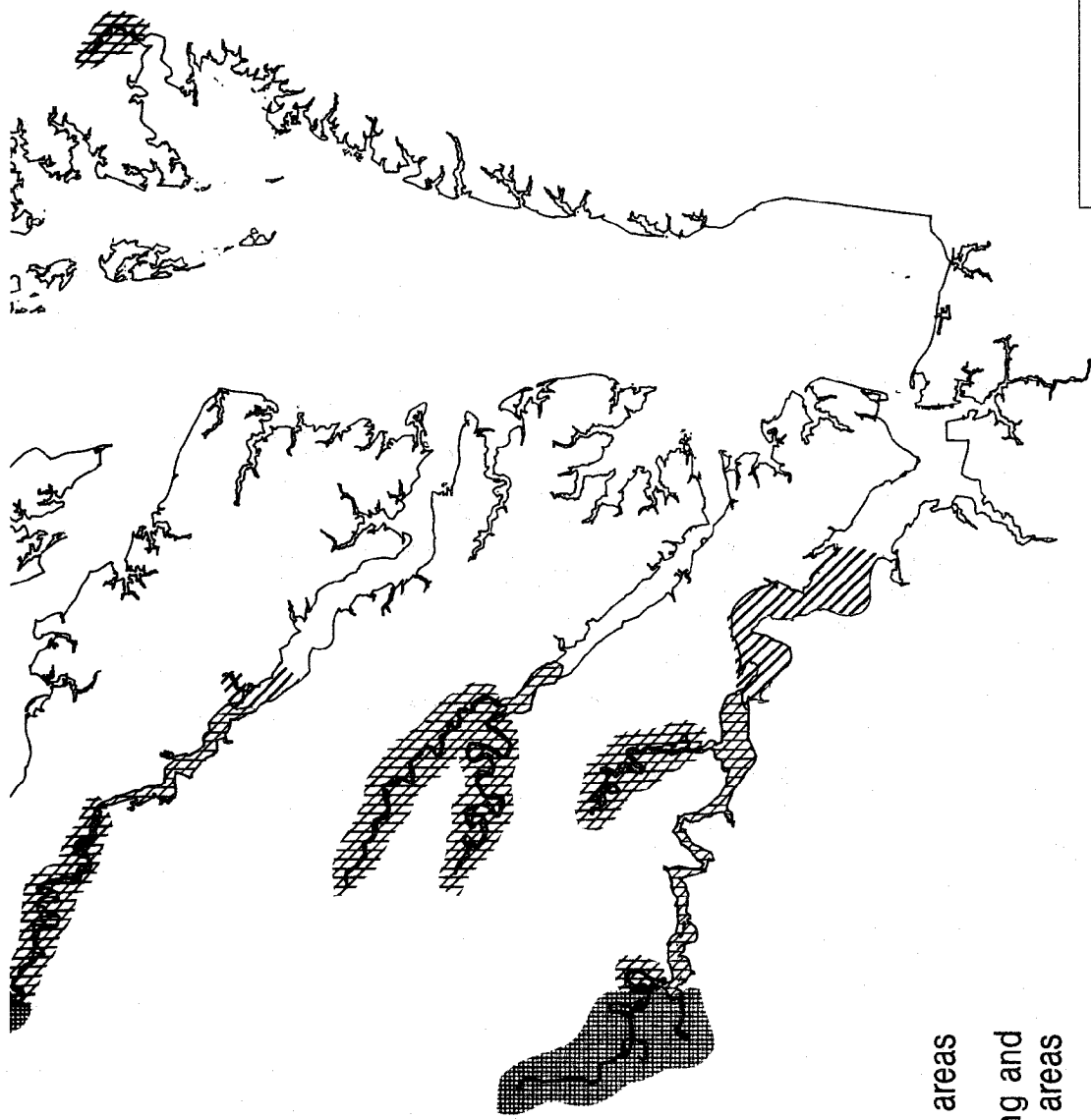
MAP 22




BLUEBACK HERRING

Alosa aestivalis

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay

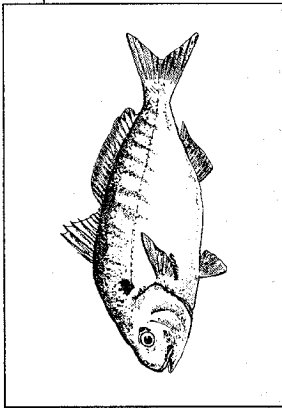




 Nursery areas
 Spawning and Nursery areas
 Potential extended distribution if blockages are removed or bypassed.

SOURCES: U.S. Army Corps of Engineers, *Chesapeake Bay Low Freshwater Inflow Study*, "Known & potential habitat" map, 1980, edited by R. Klauda based on more recent information.

Scale—1:1,069,000

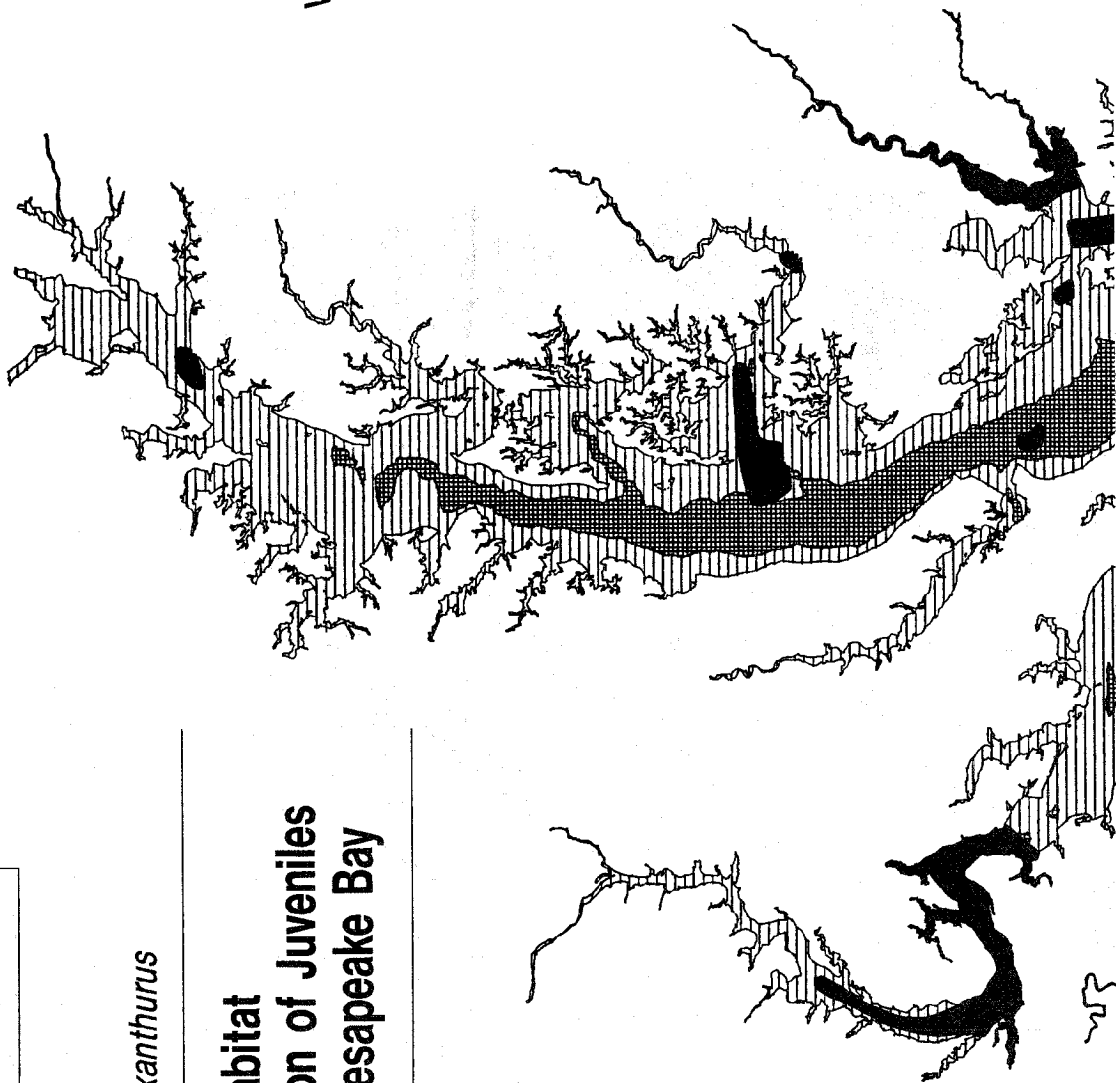


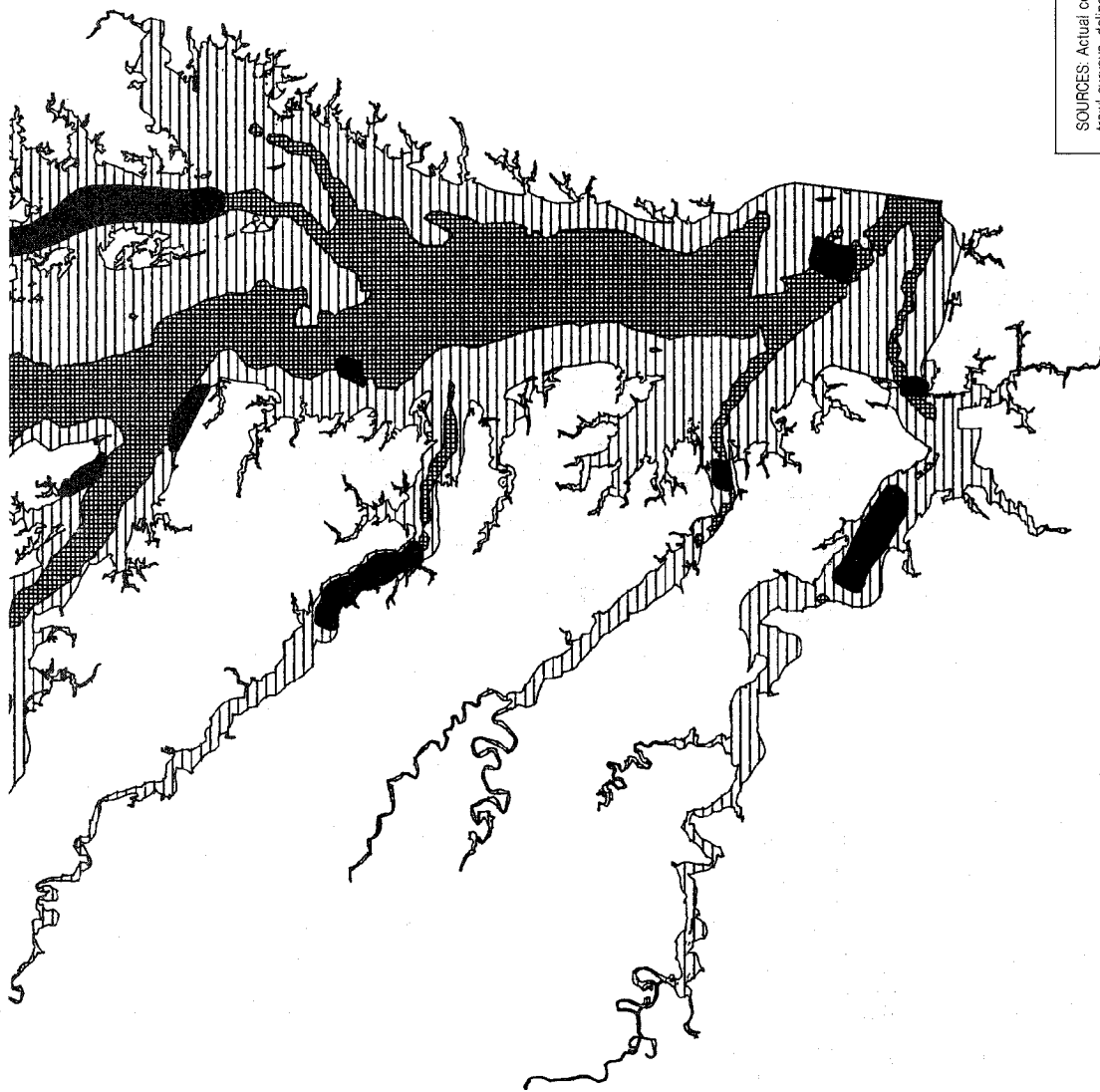
MAP 23




SPOT

Leiostomus xanthurus

Spring Habitat Distribution of Juveniles in the Chesapeake Bay

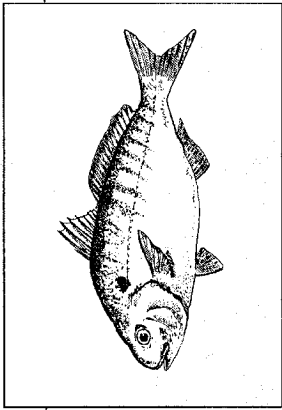




-  Actual concentrations
-  Areas of general distribution
-  Potential habitat

SOURCES: Actual concentrations from trawl surveys, delineated by M. Homer; General distribution is the rest of the Bay 10 m deep or less, where spot may occur and forage; and Potential habitat is over 10 m deep, where spot may occur but generally do not forage.

Scale—1:1,069,000

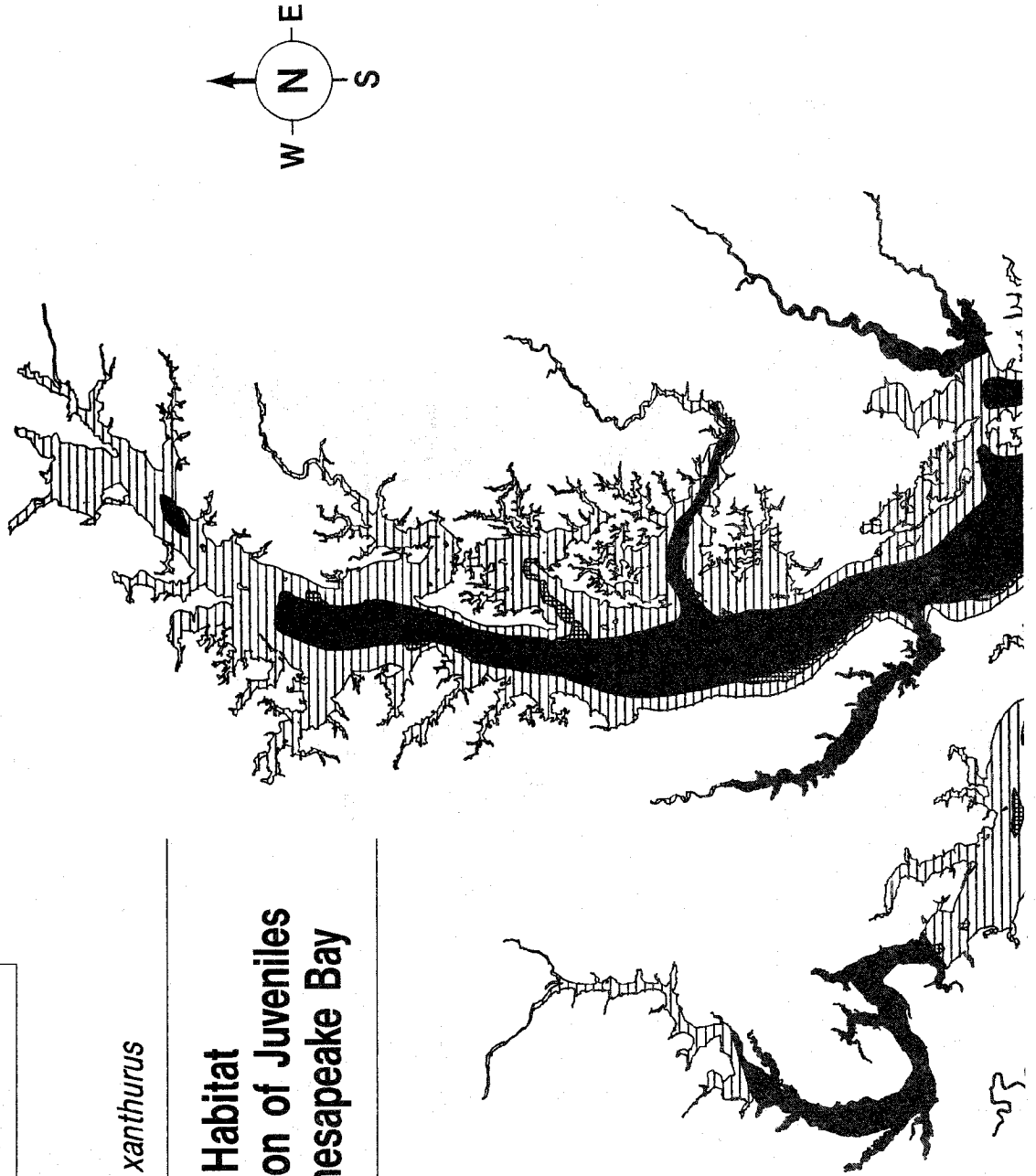


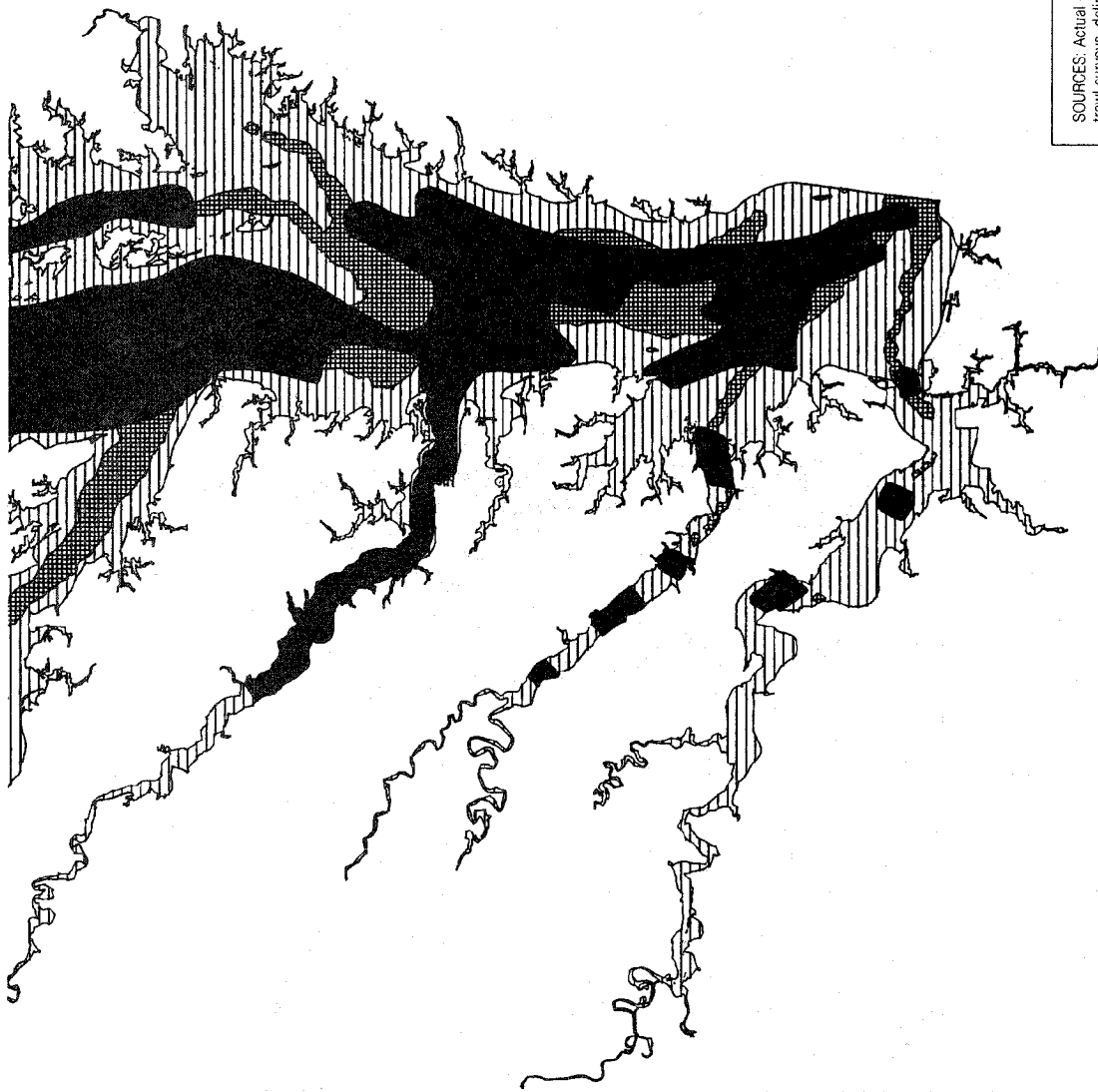
MAP 24

SPOT

Leiostomus xanthurus

Summer Habitat Distribution of Juveniles in the Chesapeake Bay

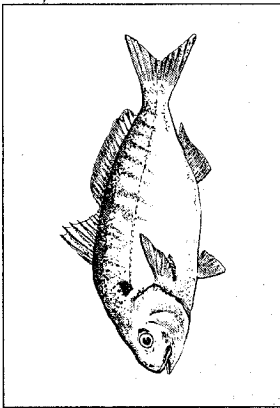




- Actual concentrations
- Areas of general distribution
- Potential habitat

SOURCES: Actual concentrations from trawl surveys, delineated by M. Homer; General distribution is the rest of the Bay 10 m deep or less, where spot may occur and forage; and Potential habitat is over 10 m deep, where spot may occur but generally do not forage.

Scale—1:1,069,000

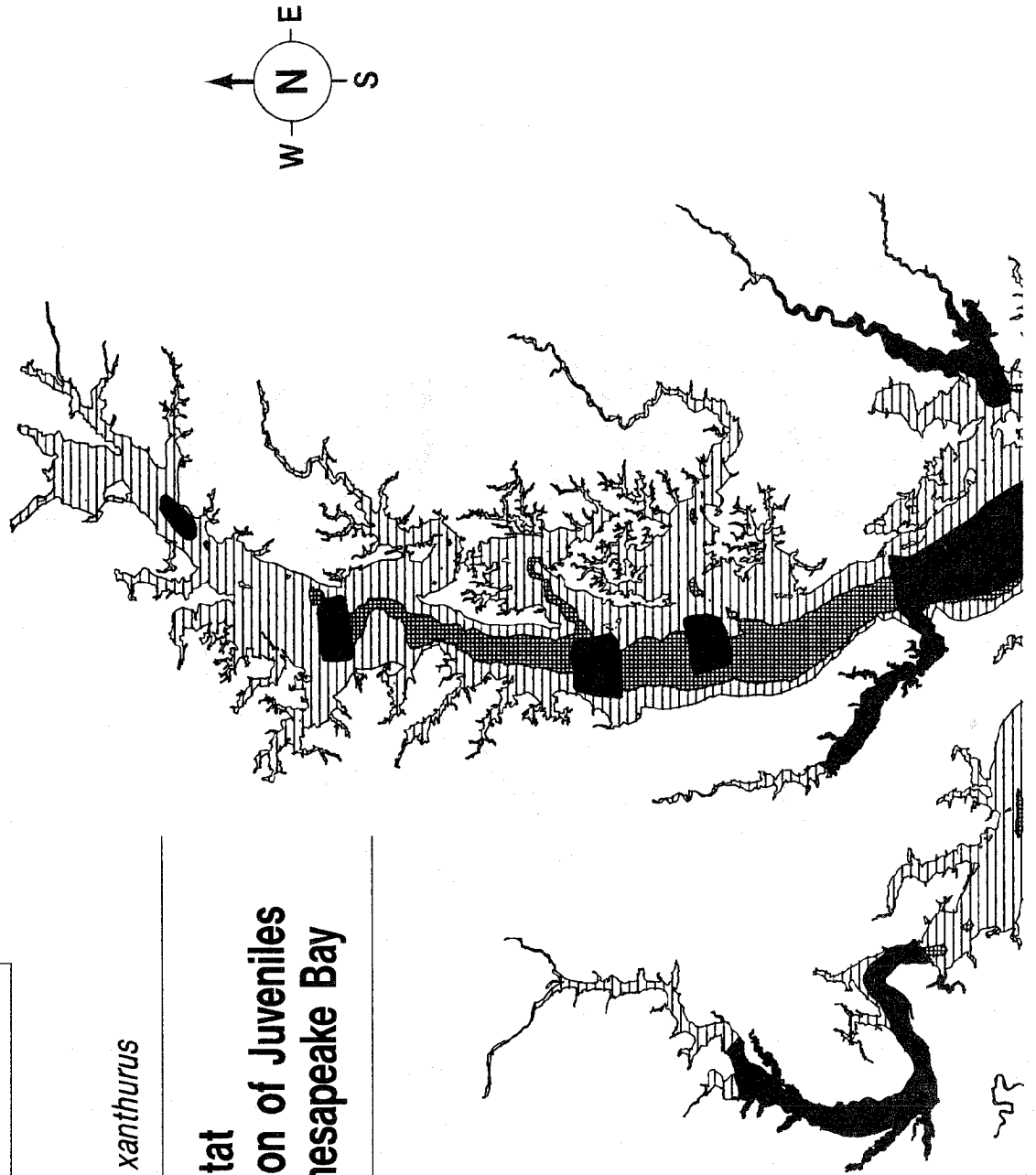


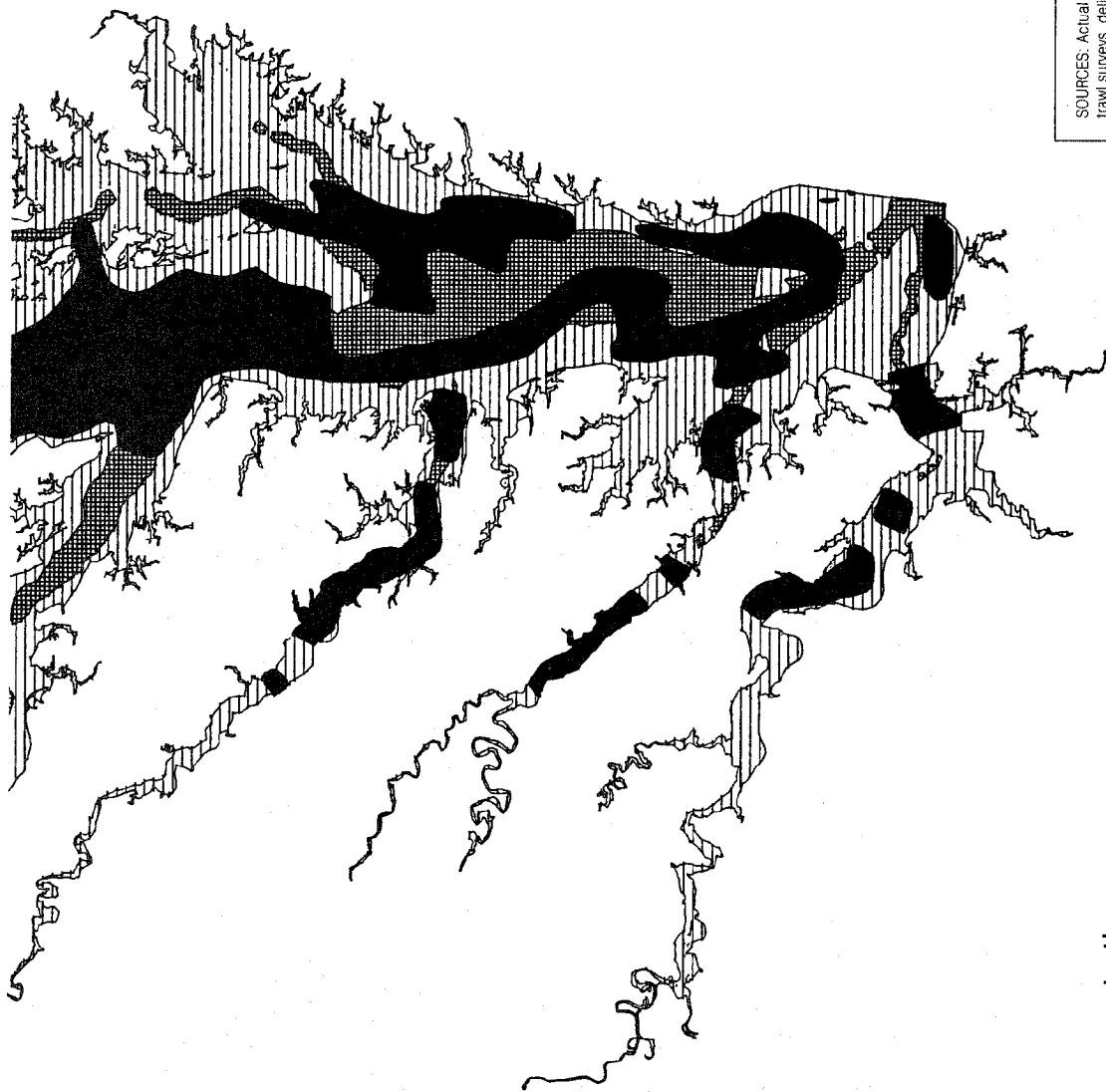
MAP 25

SPOT

Leiostomus xanthurus

Fall Habitat Distribution of Juveniles in the Chesapeake Bay

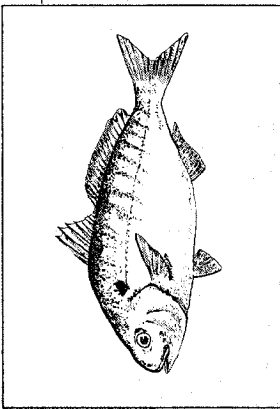




SOURCES: Actual concentrations from trawl surveys, delineated by M. Homer; General distribution is the rest of the Bay 10 m deep or less, where spot may occur and forage; and Potential habitat is over 10 m deep, where spot may occur but generally do not forage.

- Actual concentrations
- Areas of general distribution
- Potential habitat

Scale—1:1,069,000

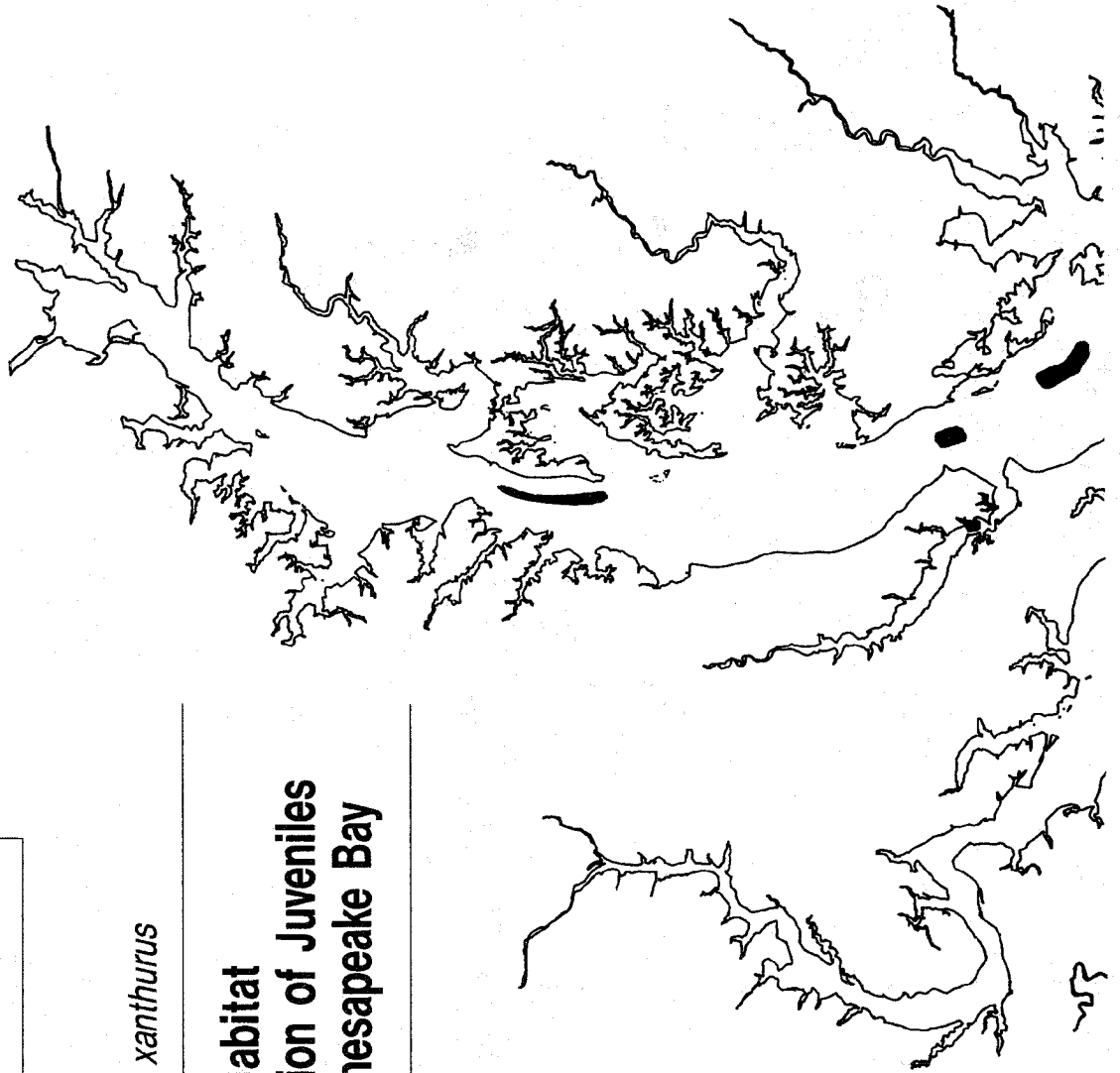
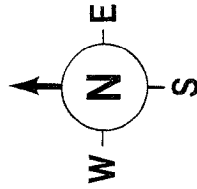


SPOT

Leiostomus xanthurus

Winter Habitat Distribution of Juveniles in the Chesapeake Bay

MAP 26

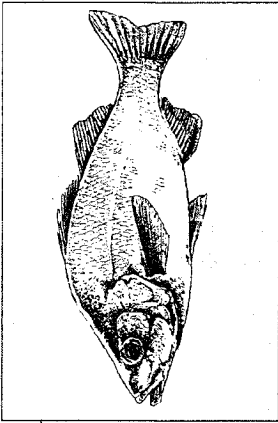




SOURCES: Actual concentrations from
trawl surveys, delineated by M. Homer.

Scale—1:1,069,000

Actual concentrations

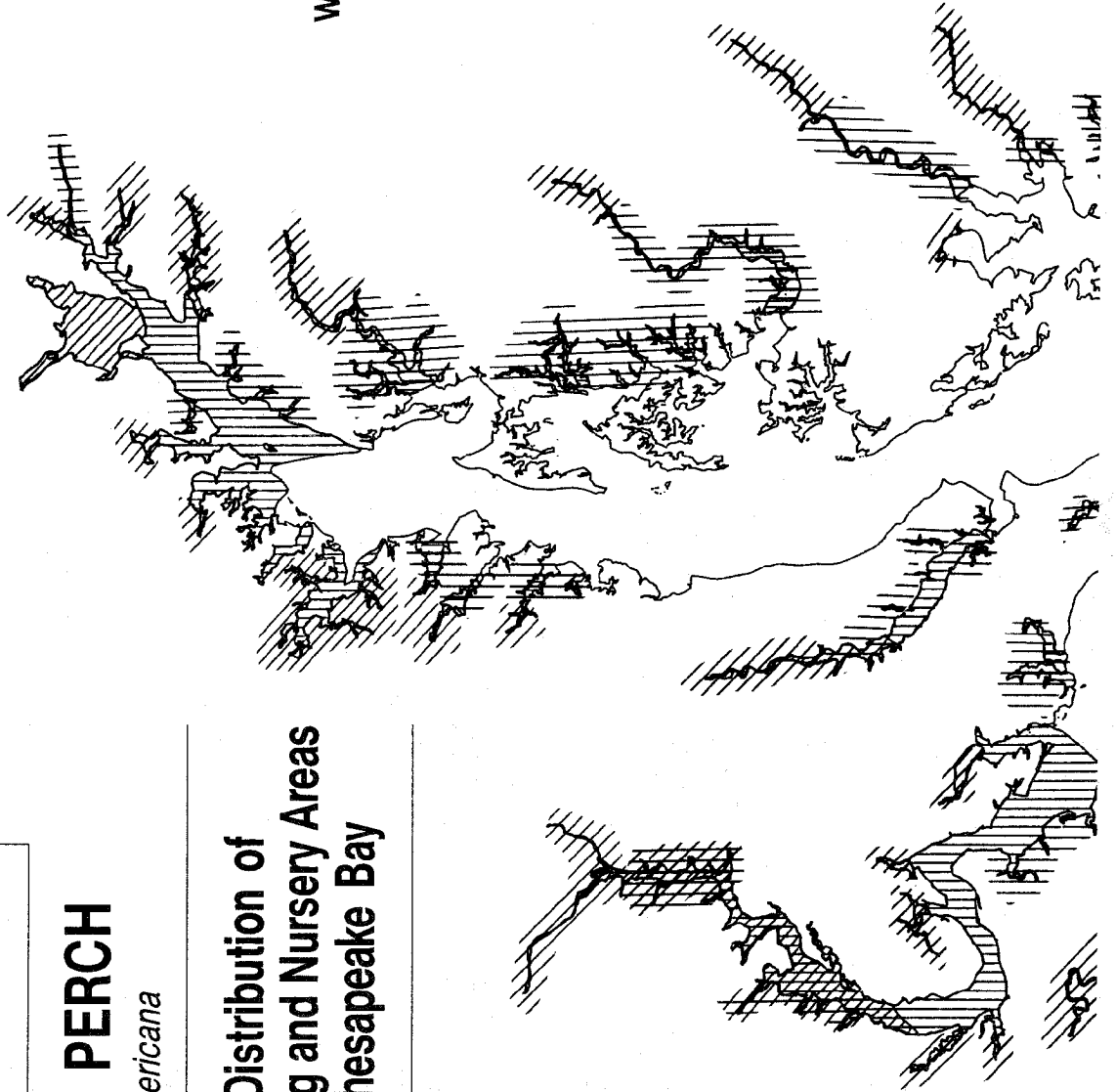


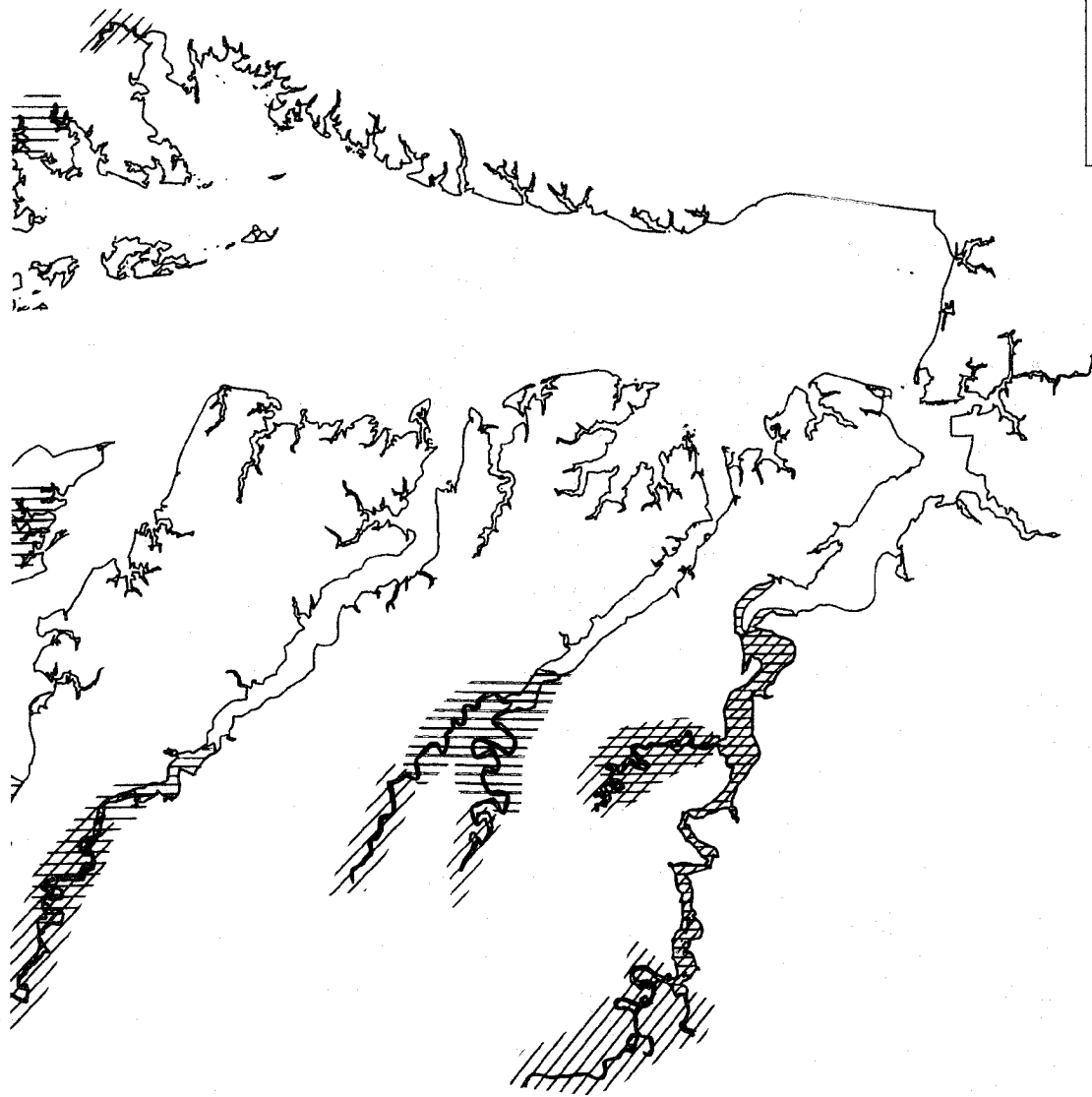
MAP 27

WHITE PERCH



Morone americana

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay

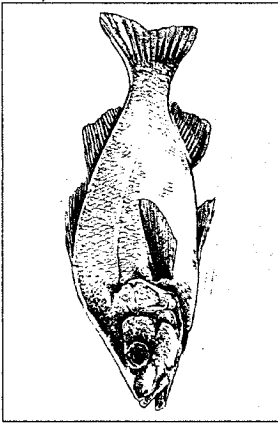




SOURCES: U.S. Army Corps of Engineers,
*Chesapeake Bay Low Freshwater Inflow
Study*, "Known & potential habitat"
map, 1980, edited by E. Seitzler-Hamilton
based on more recent information.

 Spawning area
 Nursery area

Scale—1:1,069,000

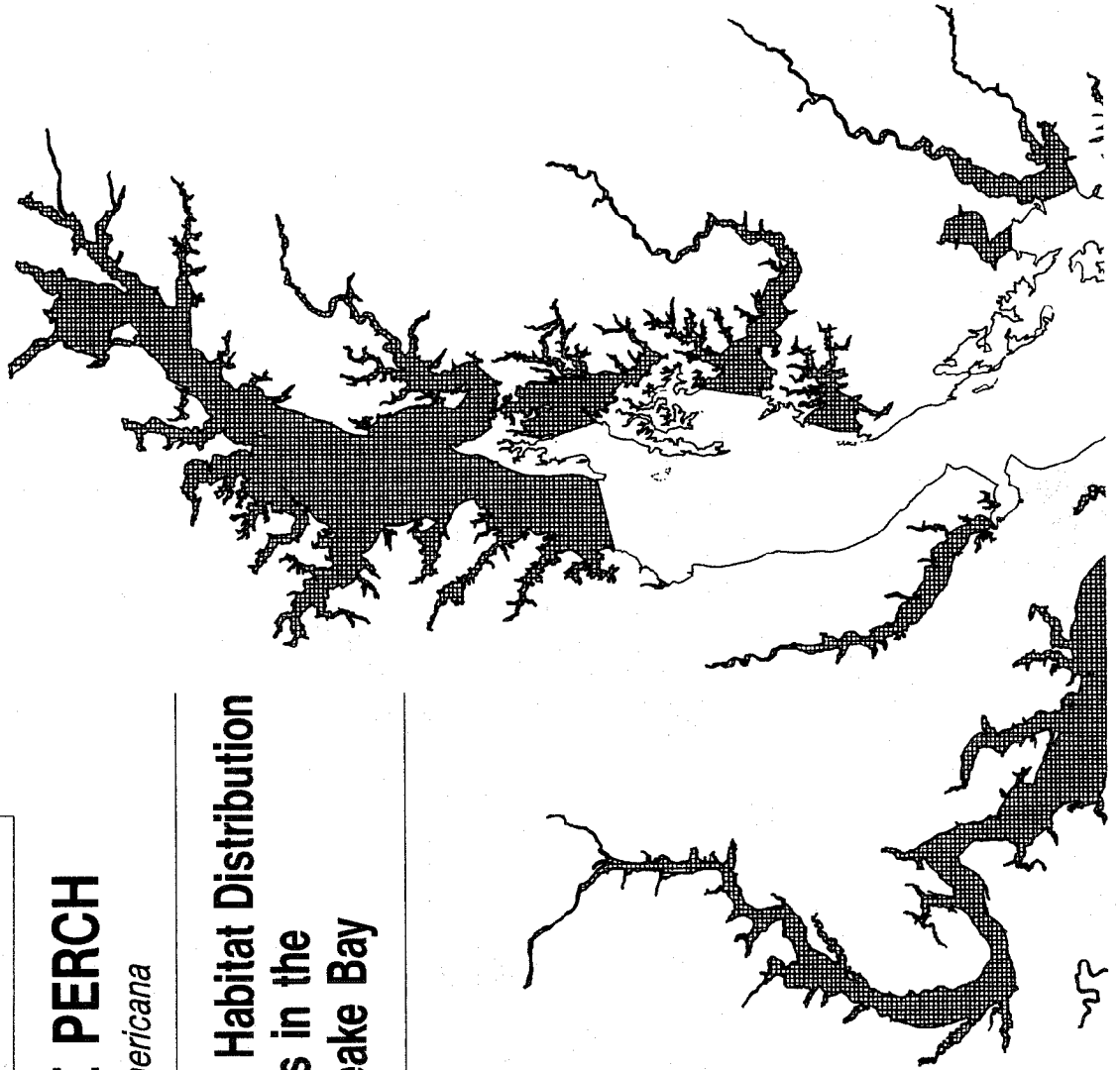
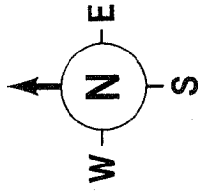


MAP 28

WHITE PERCH

Morone americana

Summer Habitat Distribution
of Adults in the
Chesapeake Bay

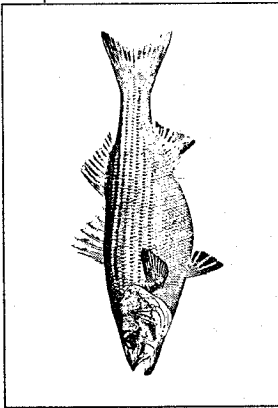




■ Summer actual/
potential distribution

(Areas with surface salinity < 10.0 .
based on 1989 July-September means)

Scale—1:1,069,000



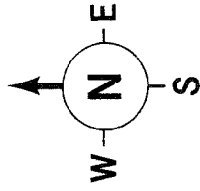
Drawings courtesy Duane Raver, Jr.

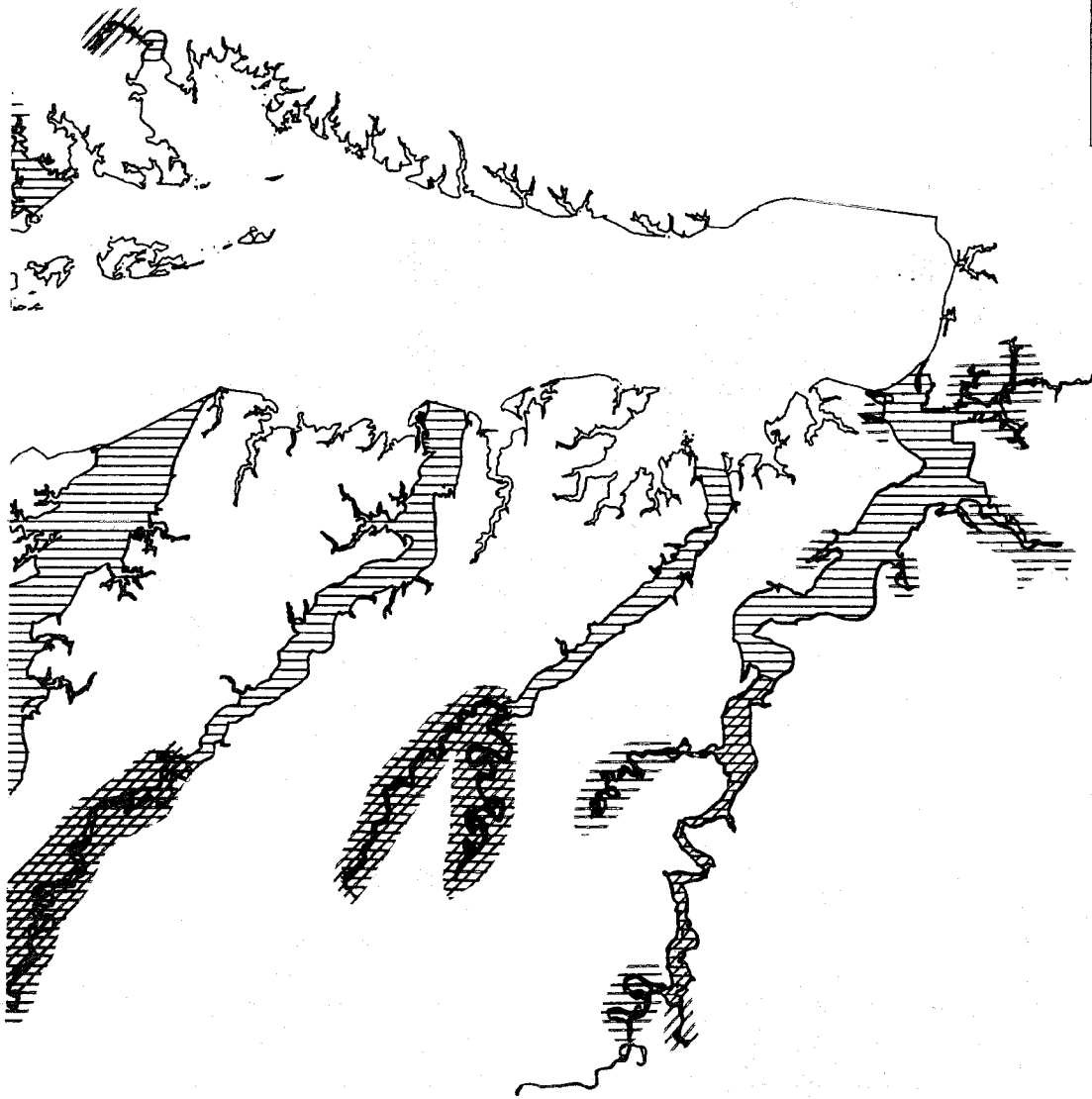
MAP 29

STRIPED BASS

Morone saxatilis

Chesapeake Bay
Spawning Reaches
and Spawning Rivers

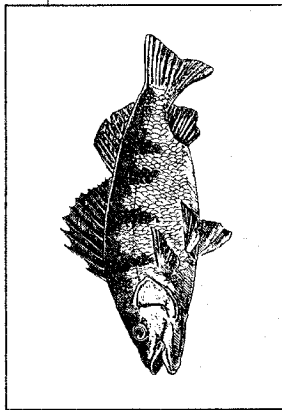




SOURCES: Legislatively defined spawning reaches and rivers, plus additional spawning reaches delineated by E. Setzler-Hamilton.

Scale—1:1,069,000

- Spawning rivers
- Spawning reaches

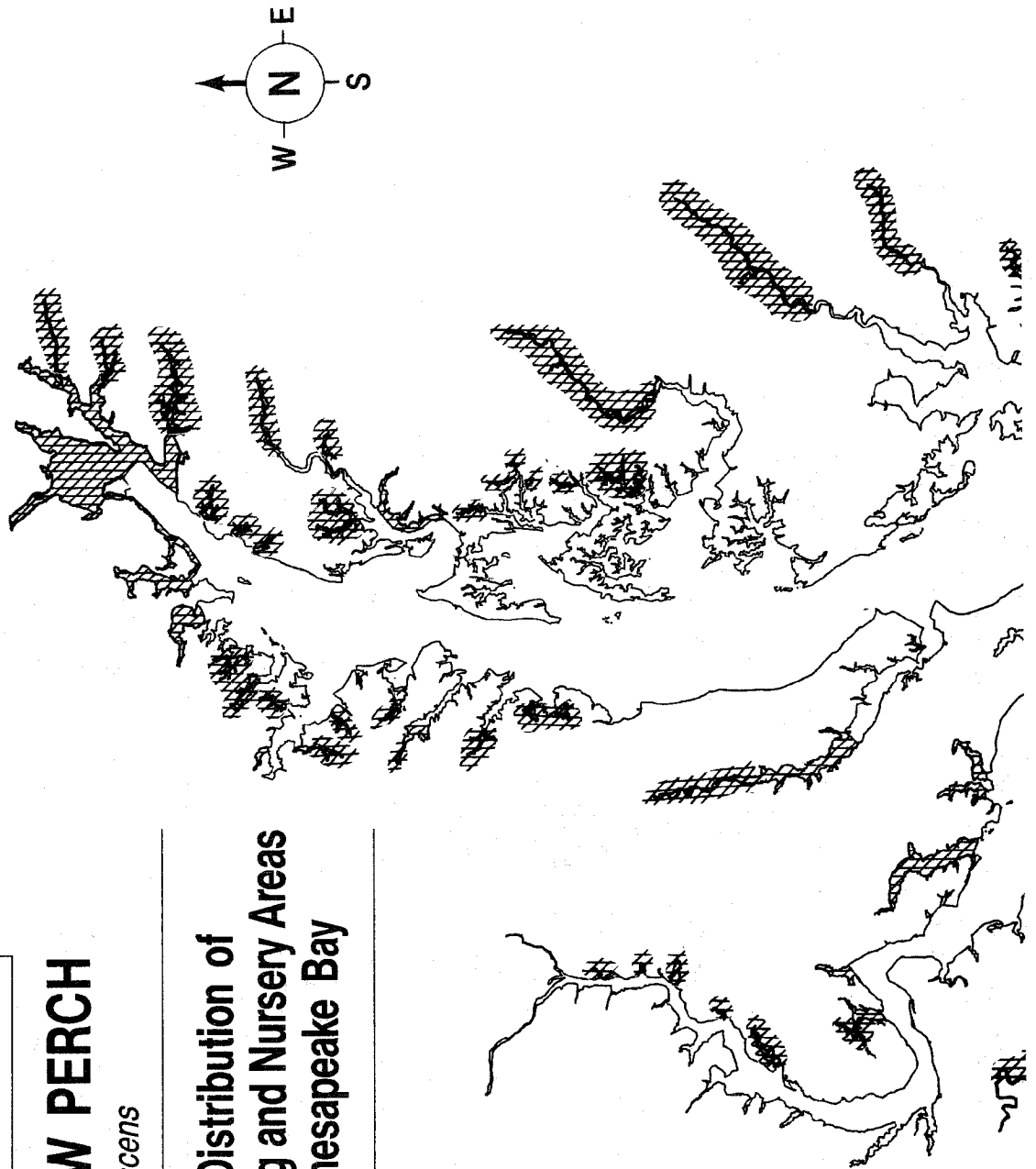


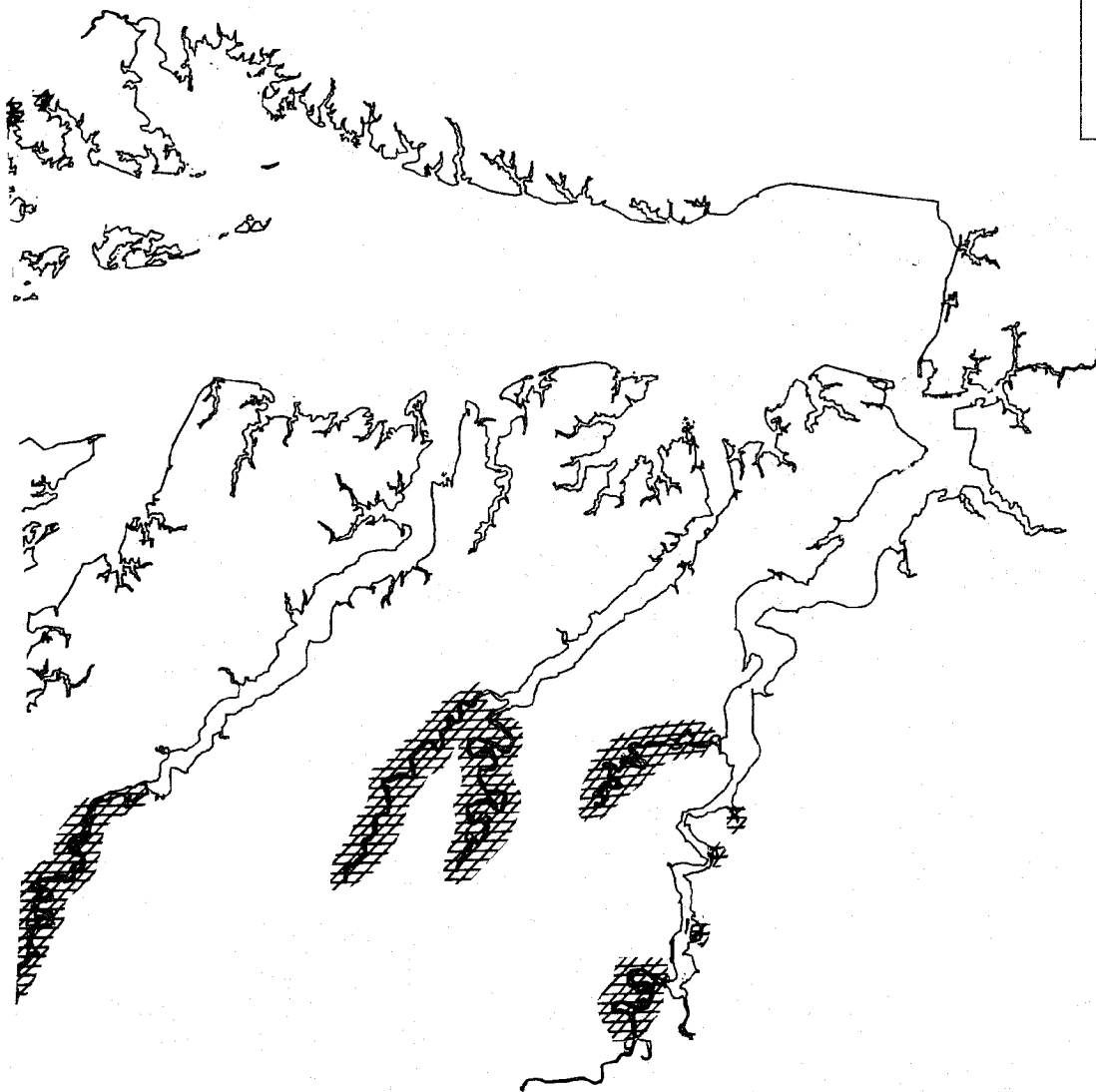
MAP 30


YELLOW PERCH

Perca flavescens

Habitat Distribution of
Spawning and Nursery Areas
in the Chesapeake Bay

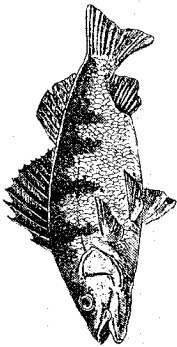
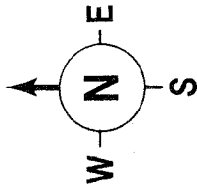




 Nursery / Spawning
areas

SOURCES: U.S. Army Corps of Engineers,
Chesapeake Bay Low Freshwater Inflow
Study, "Known & potential habitat"
map, 1980, edited by P. Plavis based
on more recent information.

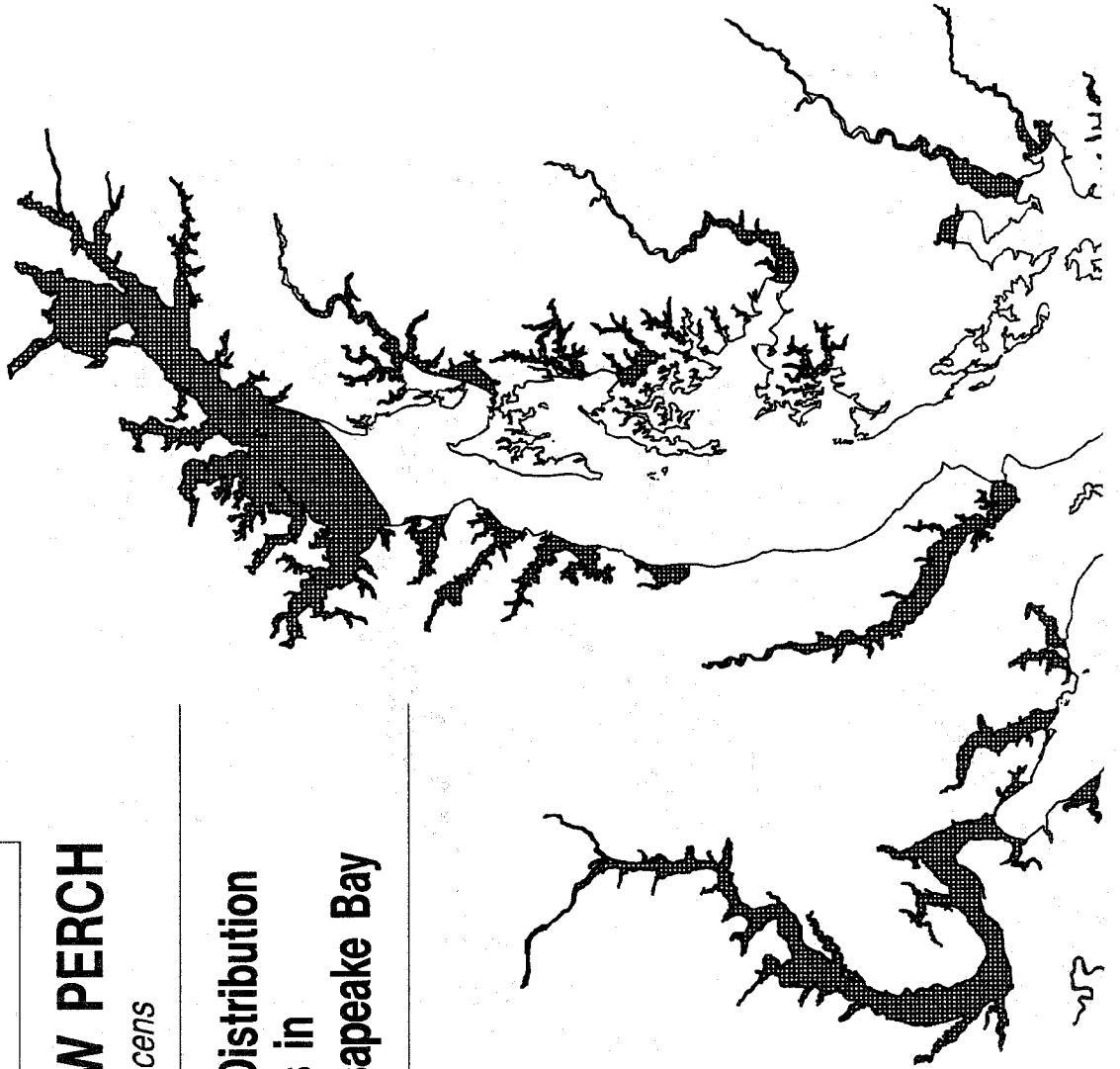
Scale—1:1,069,000

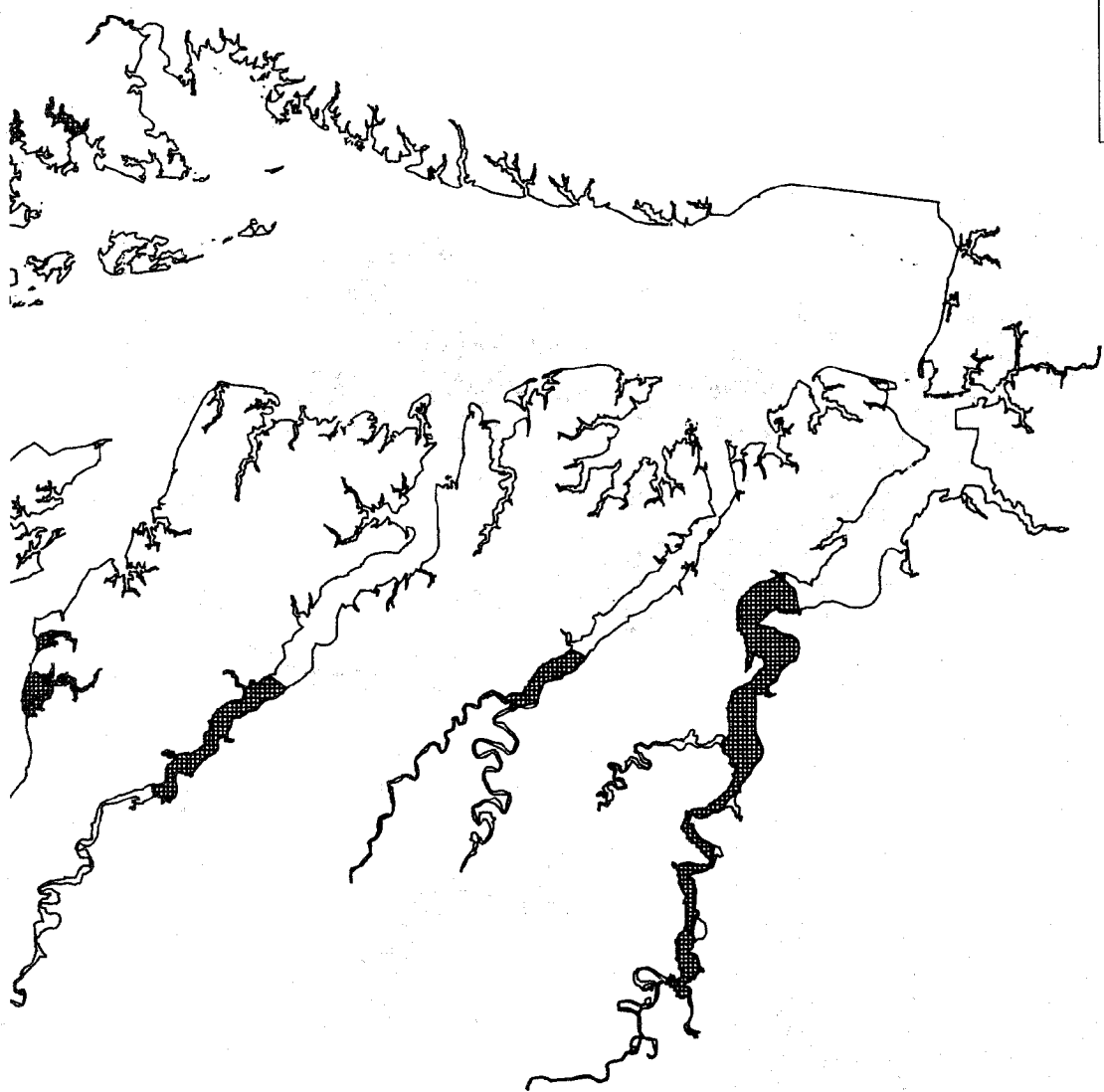


YELLOW PERCH

Perca flavescens

Habitat Distribution
of Adults in
the Chesapeake Bay

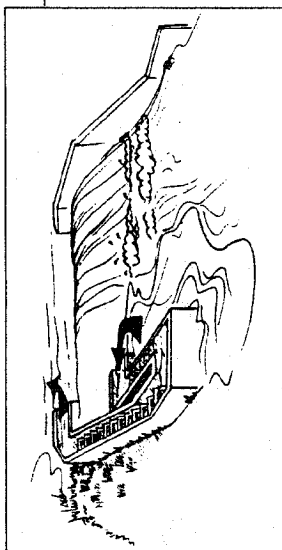




■ Adult actual/Potential
distribution

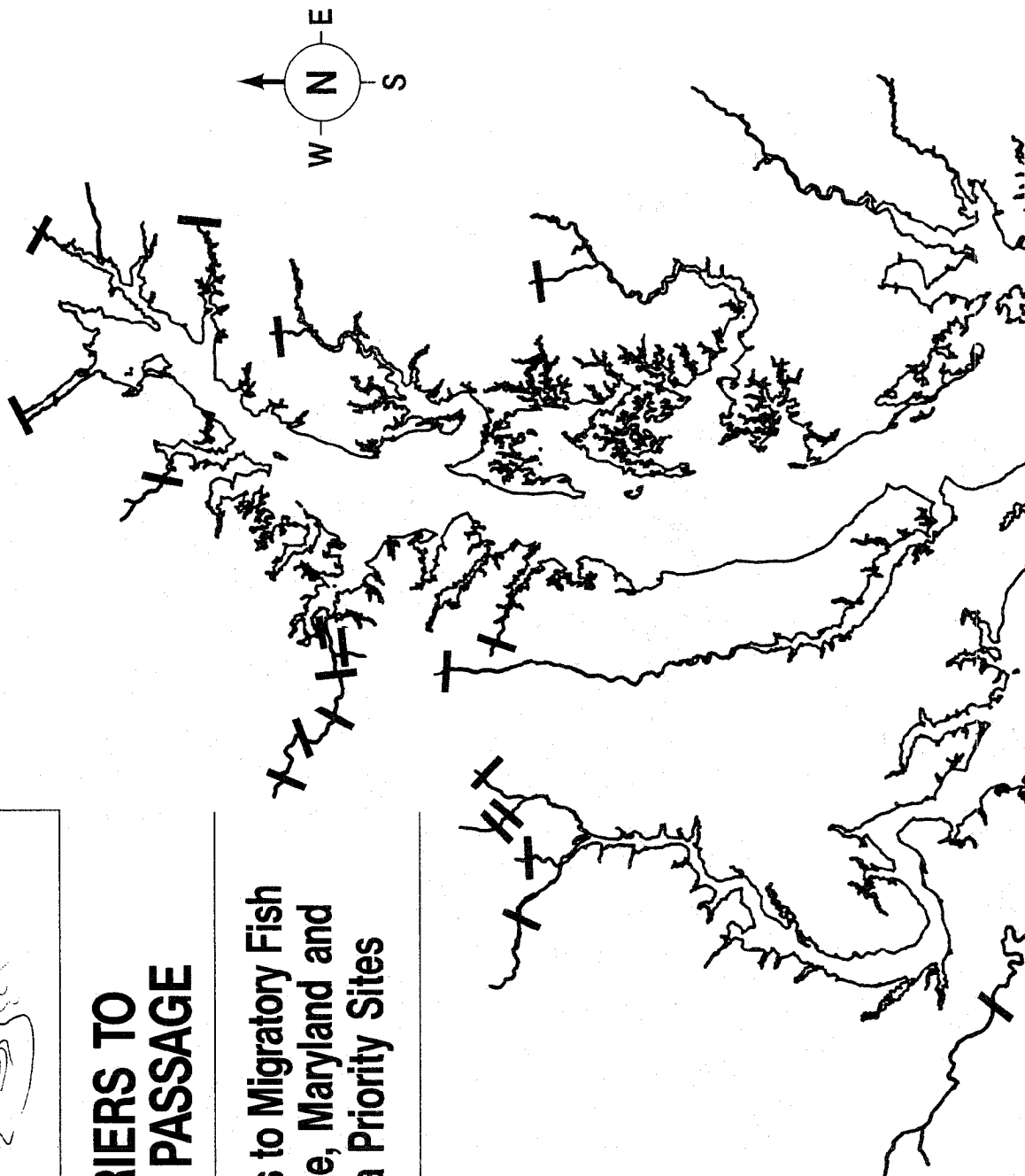
SOURCES: U.S. Army Corps of Engineers,
Chesapeake Bay Low Freshwater Inflow
Study, "Known & potential habitat"
map, 1980, edited by P. Plavis based
on more recent information.

Scale—1:1,069,000



BARRIERS TO FISH PASSAGE

Barriers to Migratory Fish Passage, Maryland and Virginia Priority Sites



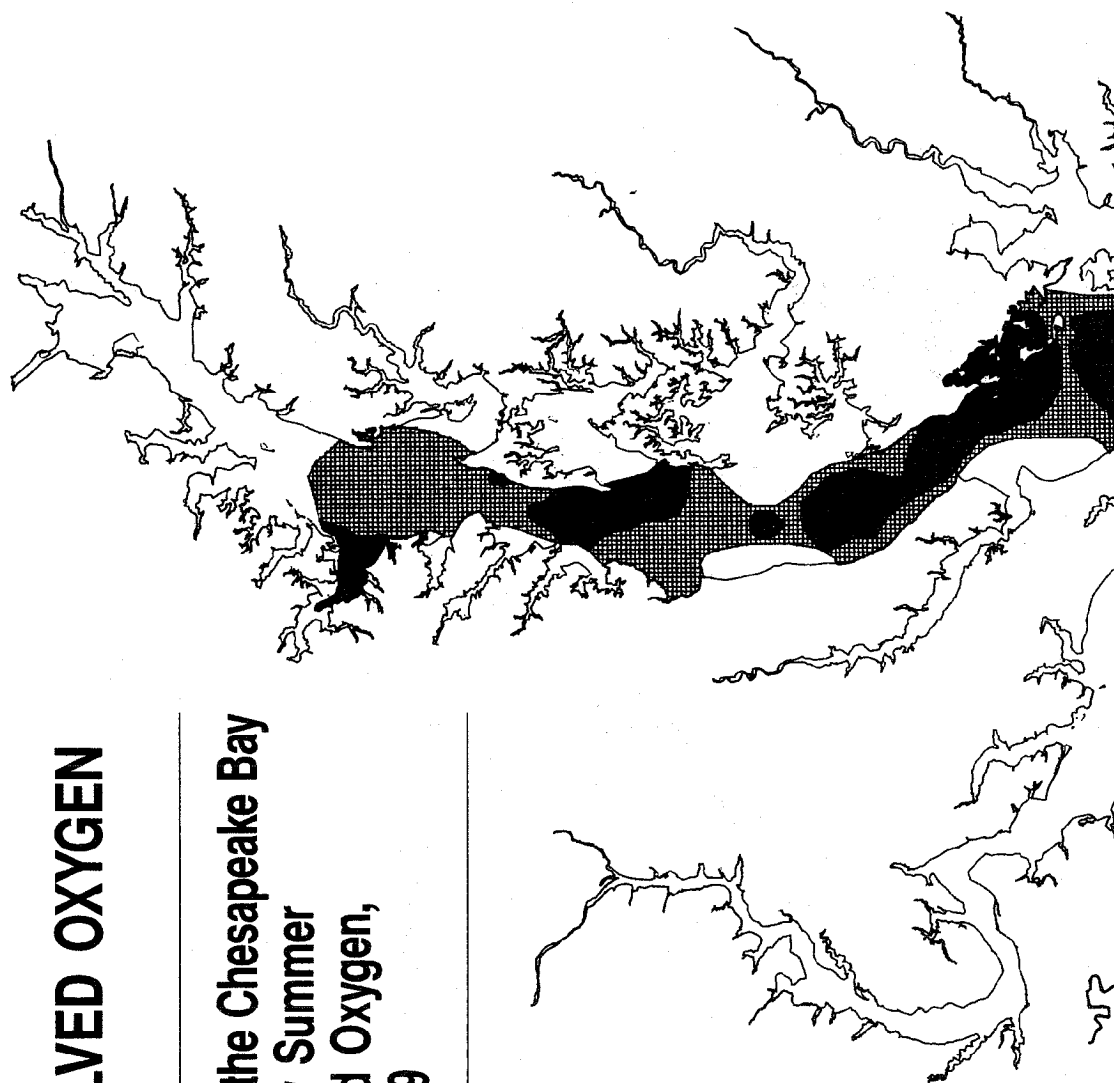


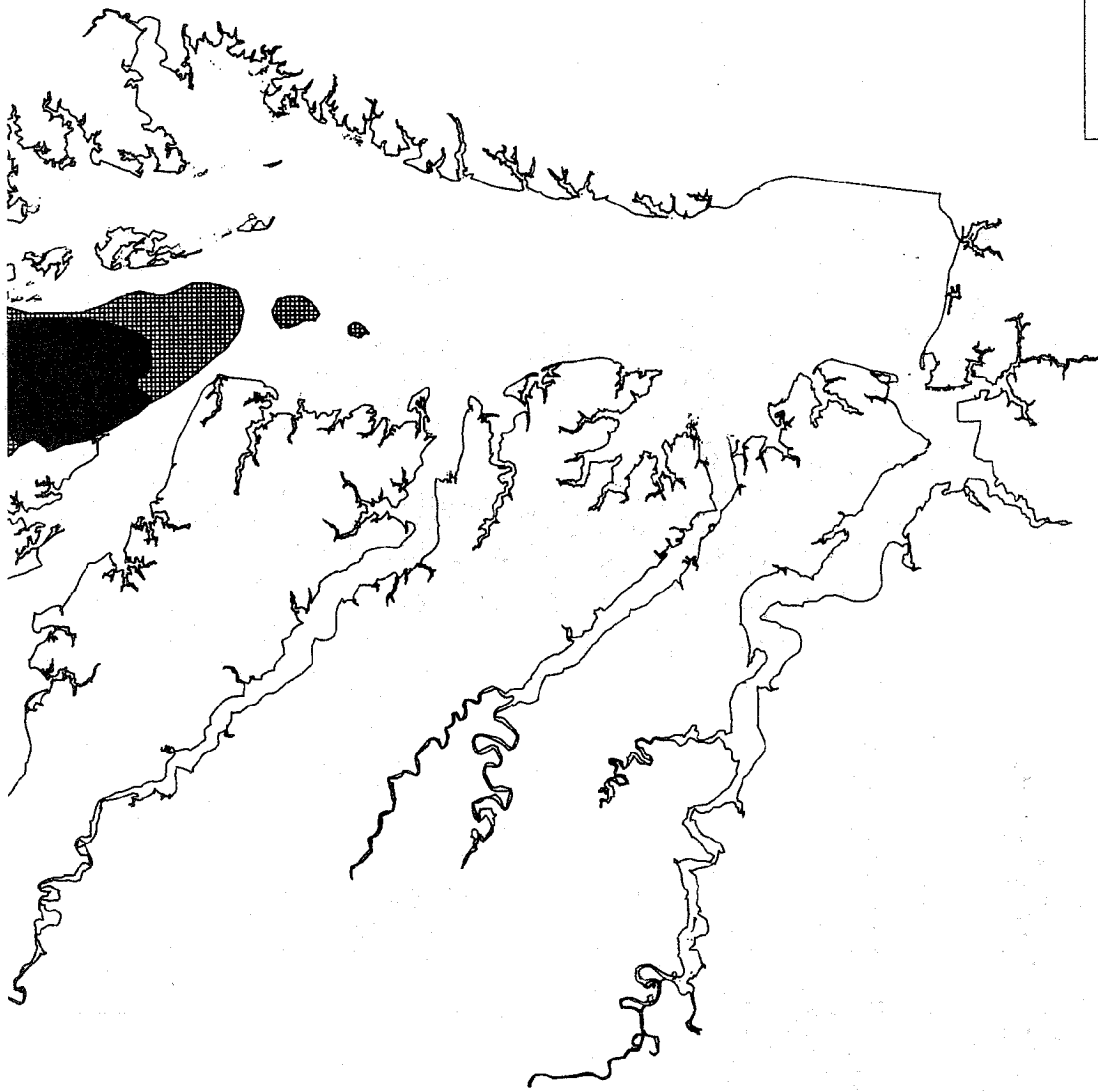
— Dam blocking fish passage



Scale—1:1,069,000

DISSOLVED OXYGEN

Areas of the Chesapeake Bay
with Low Summer
Dissolved Oxygen,
1985-1989



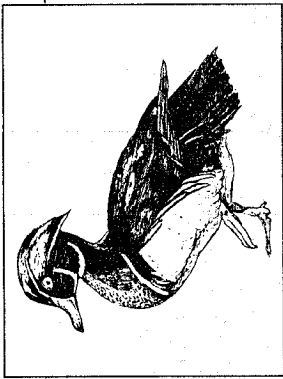


 < 2 mg/l DO
 < 3 mg/l DO

Primarily affects menhaden, spot, bay anchovy, blue crab, and striped bass.

SOURCE: 1985-89 July-September mean DO, for all below pycnocline samples from mainstem stations. Low summer DO occurs in the tributaries, but was not mapped.

Scale—1:1,069,000

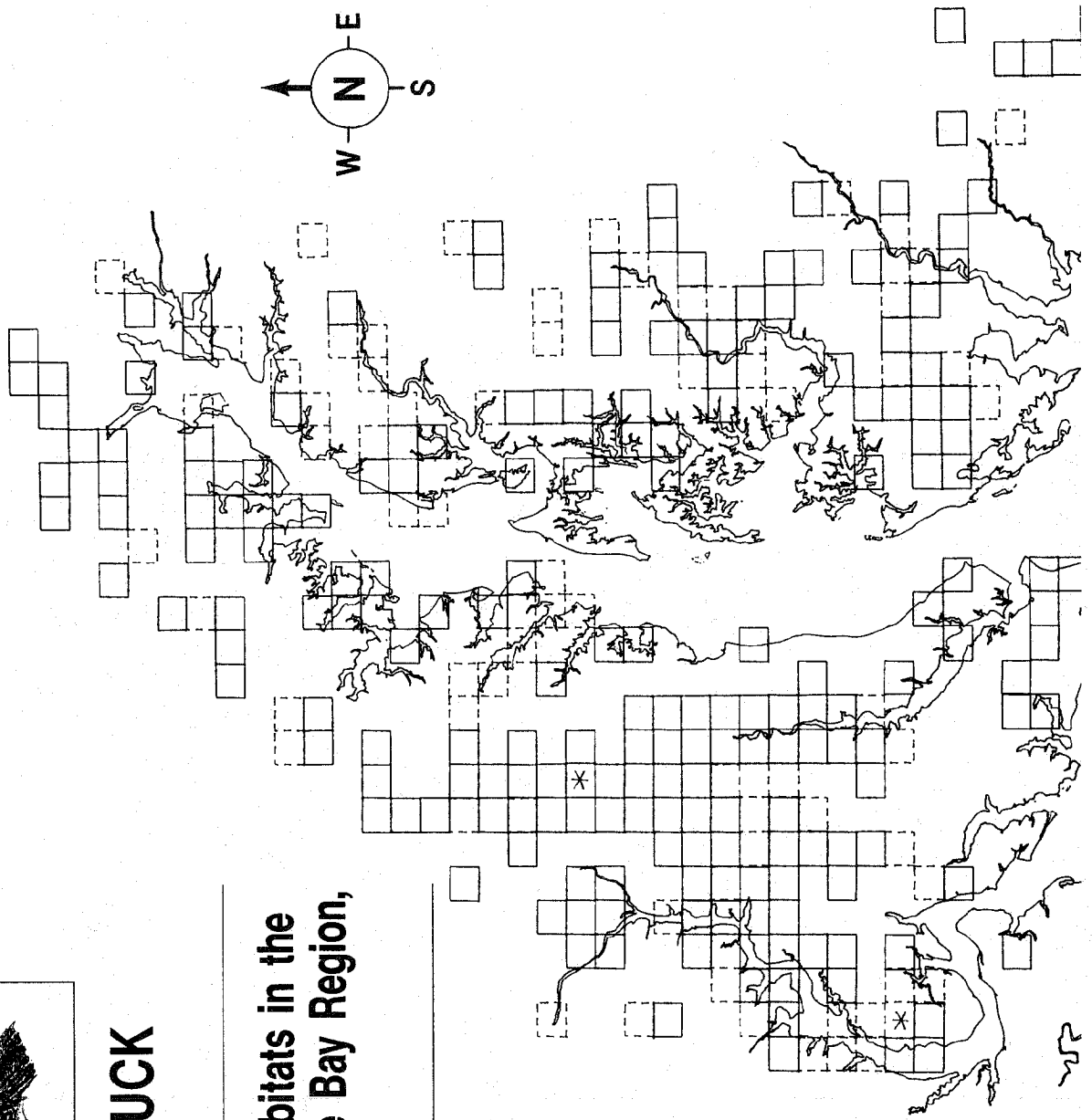


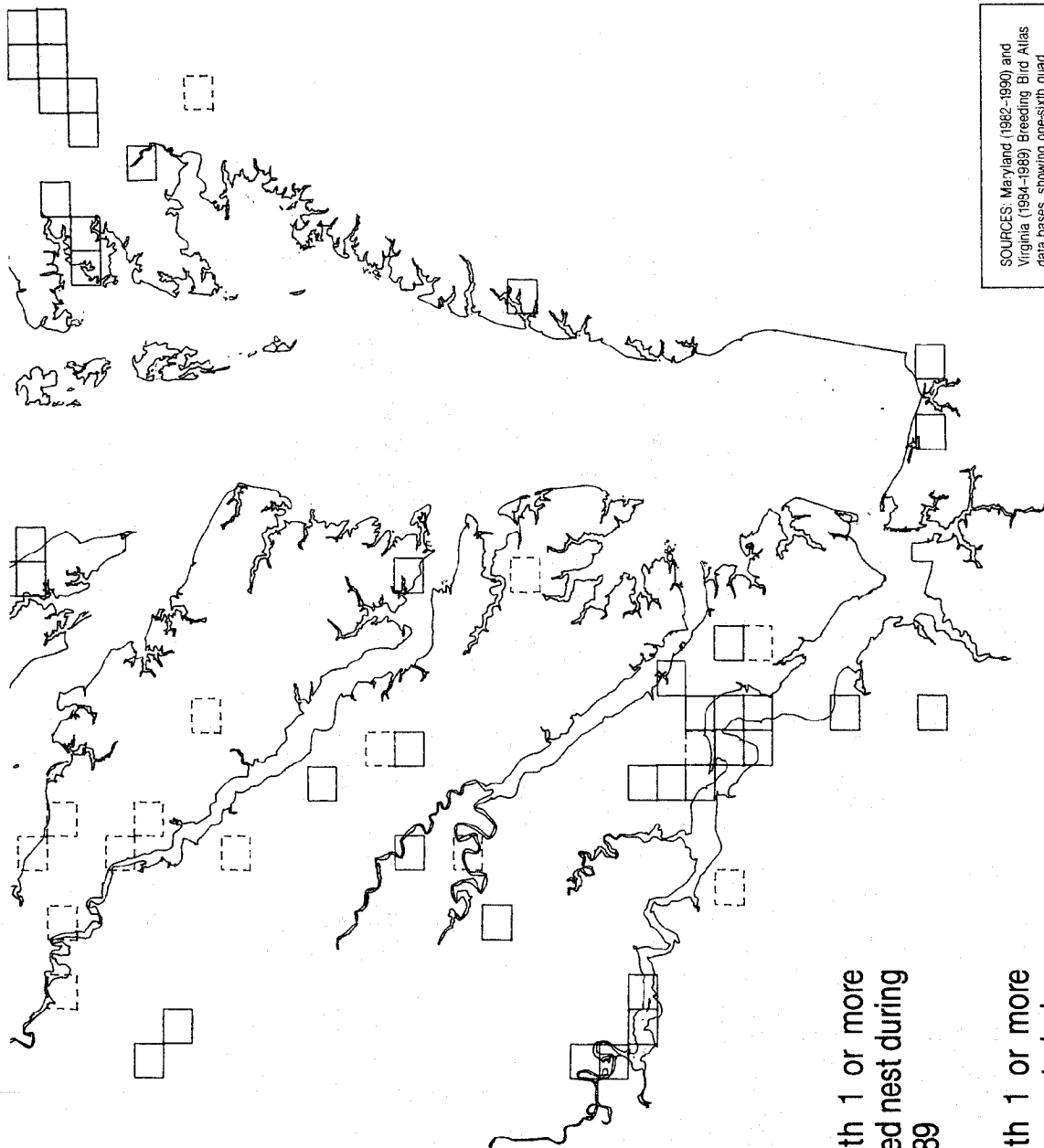
WOOD DUCK


Aix sponsa


Nesting Habitats in the
Chesapeake Bay Region,
1982-1989

MAP 34





 Area with 1 or more confirmed nest during 1982-1989

 Area with 1 or more probable nest during 1982-1989

 Area without nest

SOURCES: Maryland (1982-1990) and Virginia (1984-1989) Breeding Bird Atlas data bases, showing one-sixth quad blocks with confirmed nesting. Blocks with asterisks did not have nests, but appeared to because adjoining areas had nests.

Scale—1:1,069,000

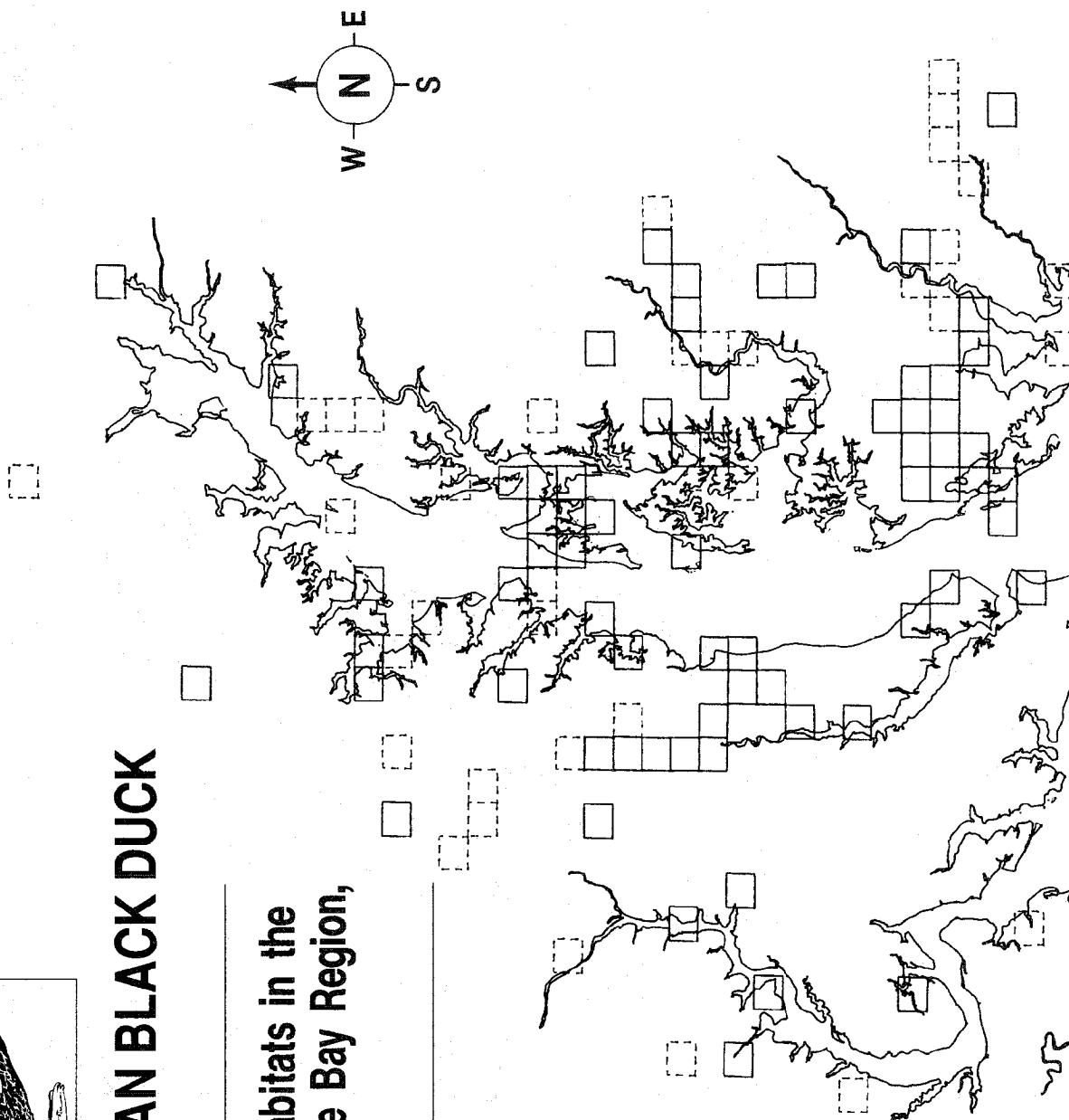


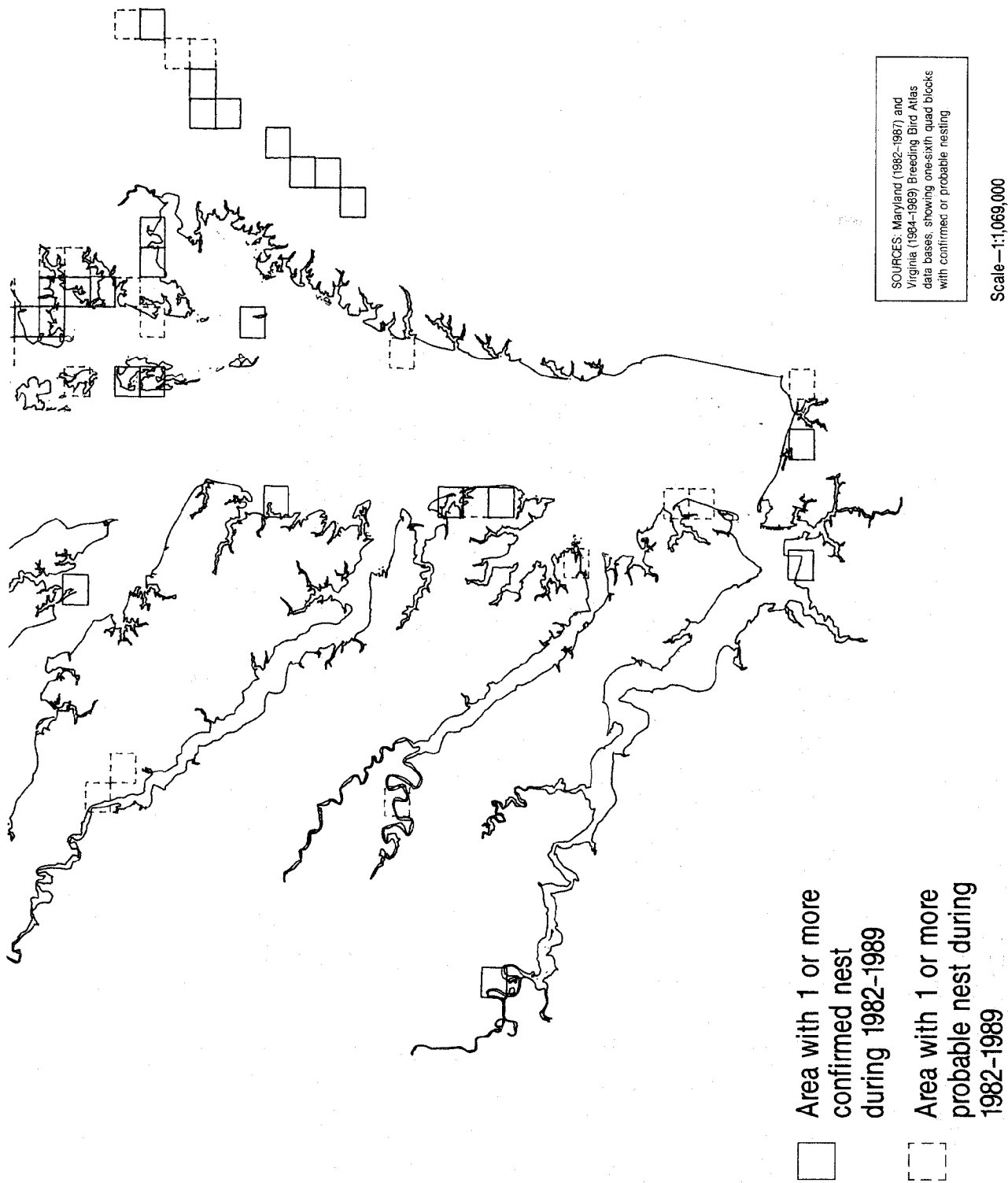
MAP 35

AMERICAN BLACK DUCK

Anas rubripes

Nesting Habitats in the
Chesapeake Bay Region,
1982-1989





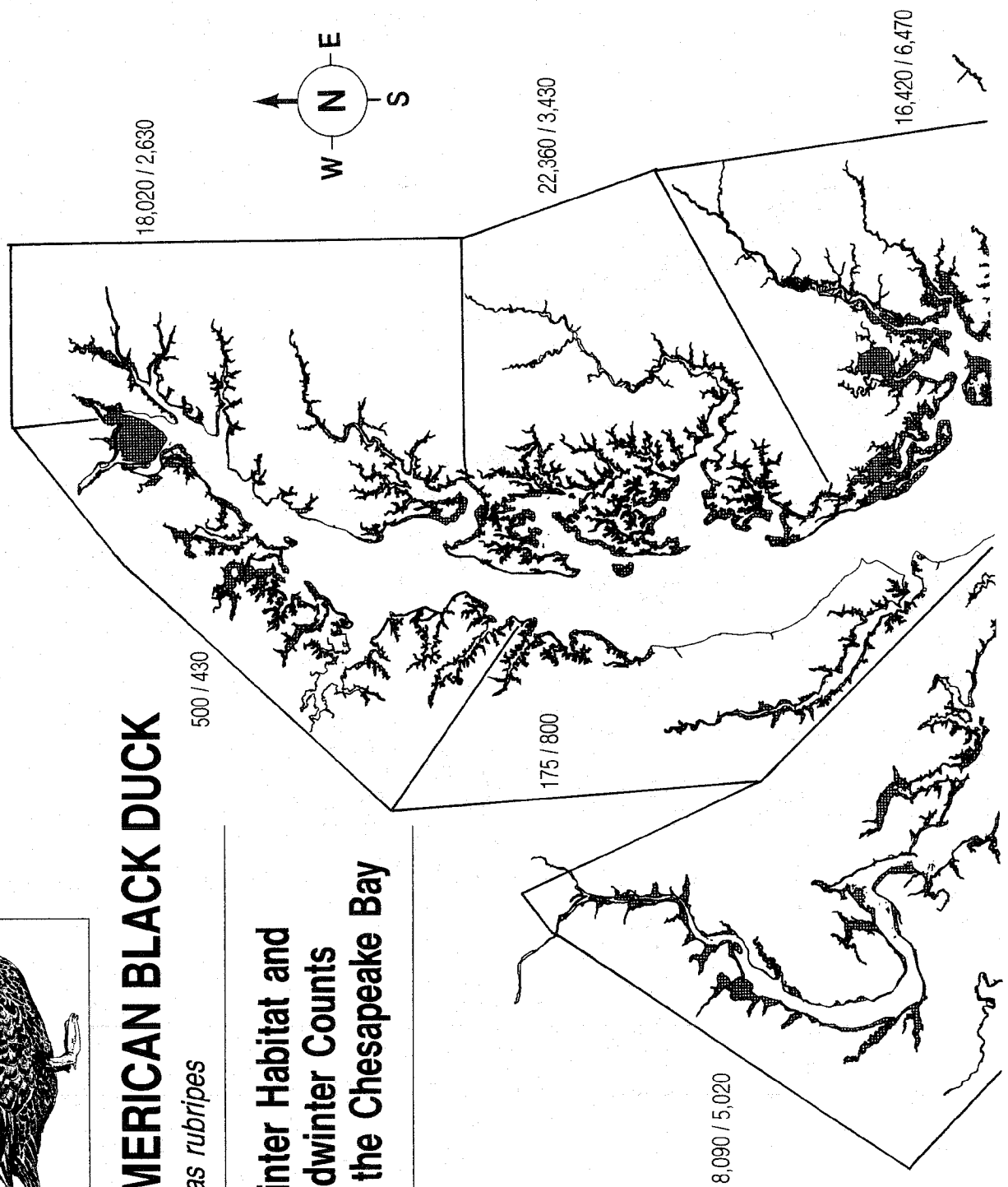


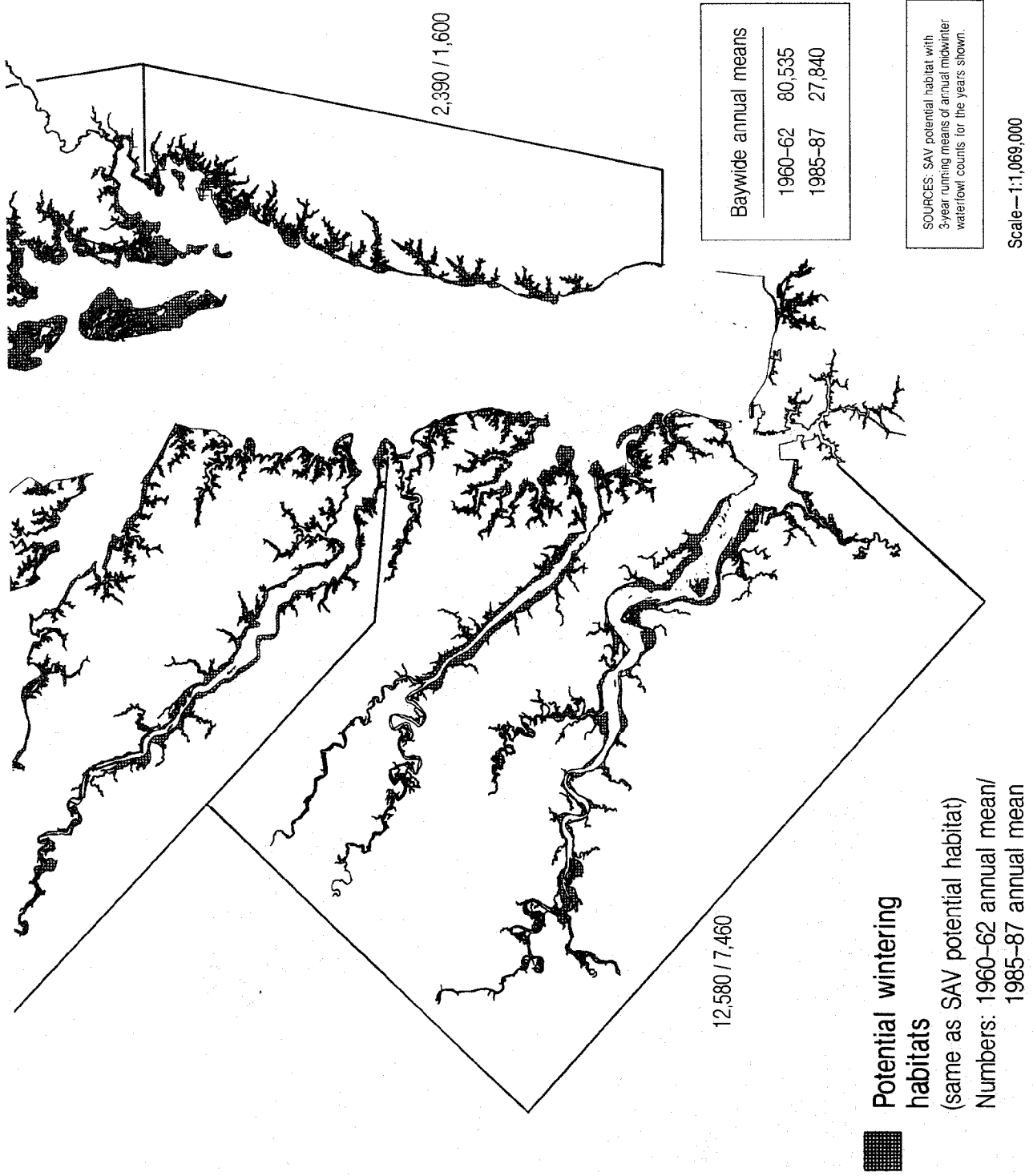
AMERICAN BLACK DUCK

Anas rubripes

Winter Habitat and
Midwinter Counts
in the Chesapeake Bay

MAP 36





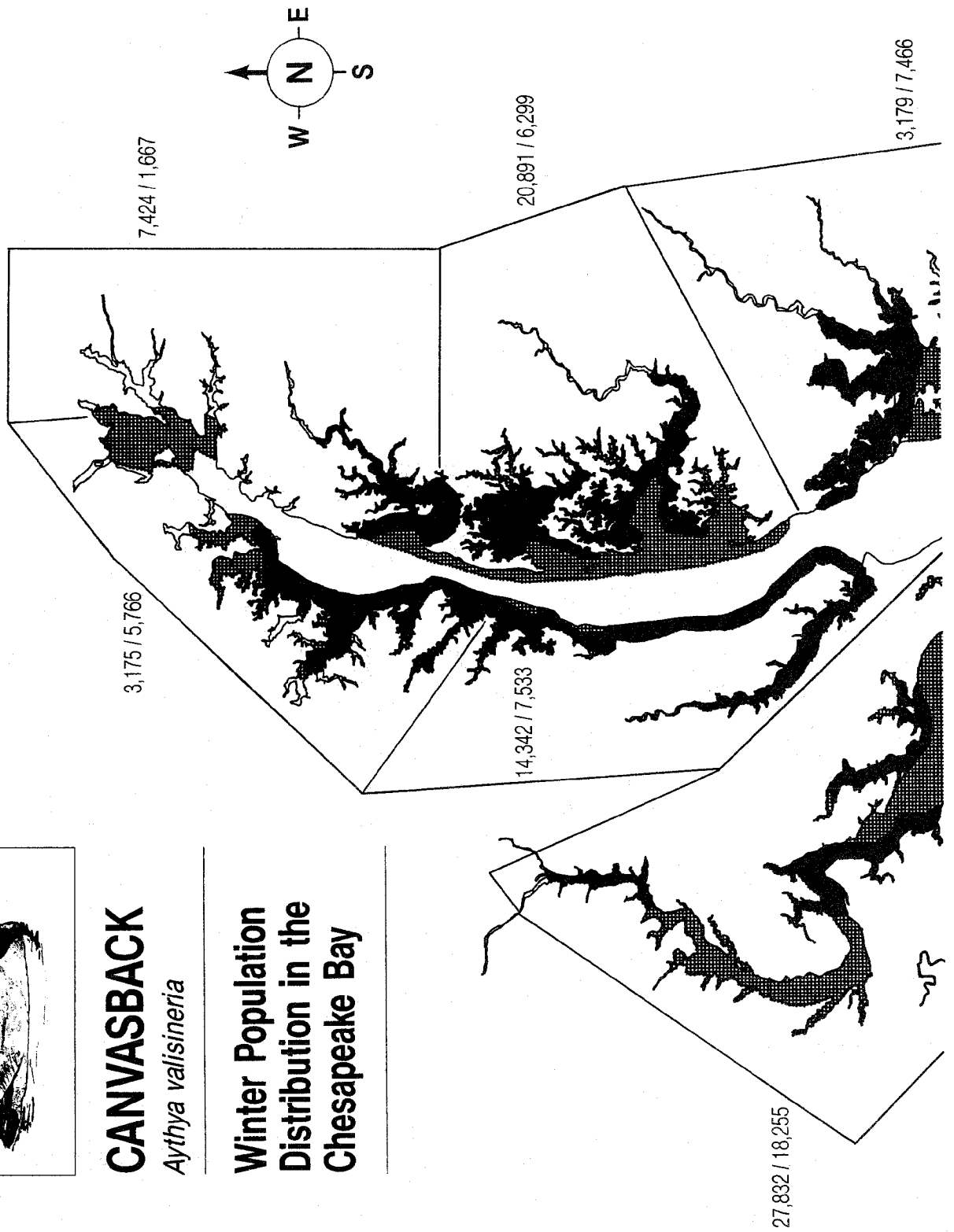


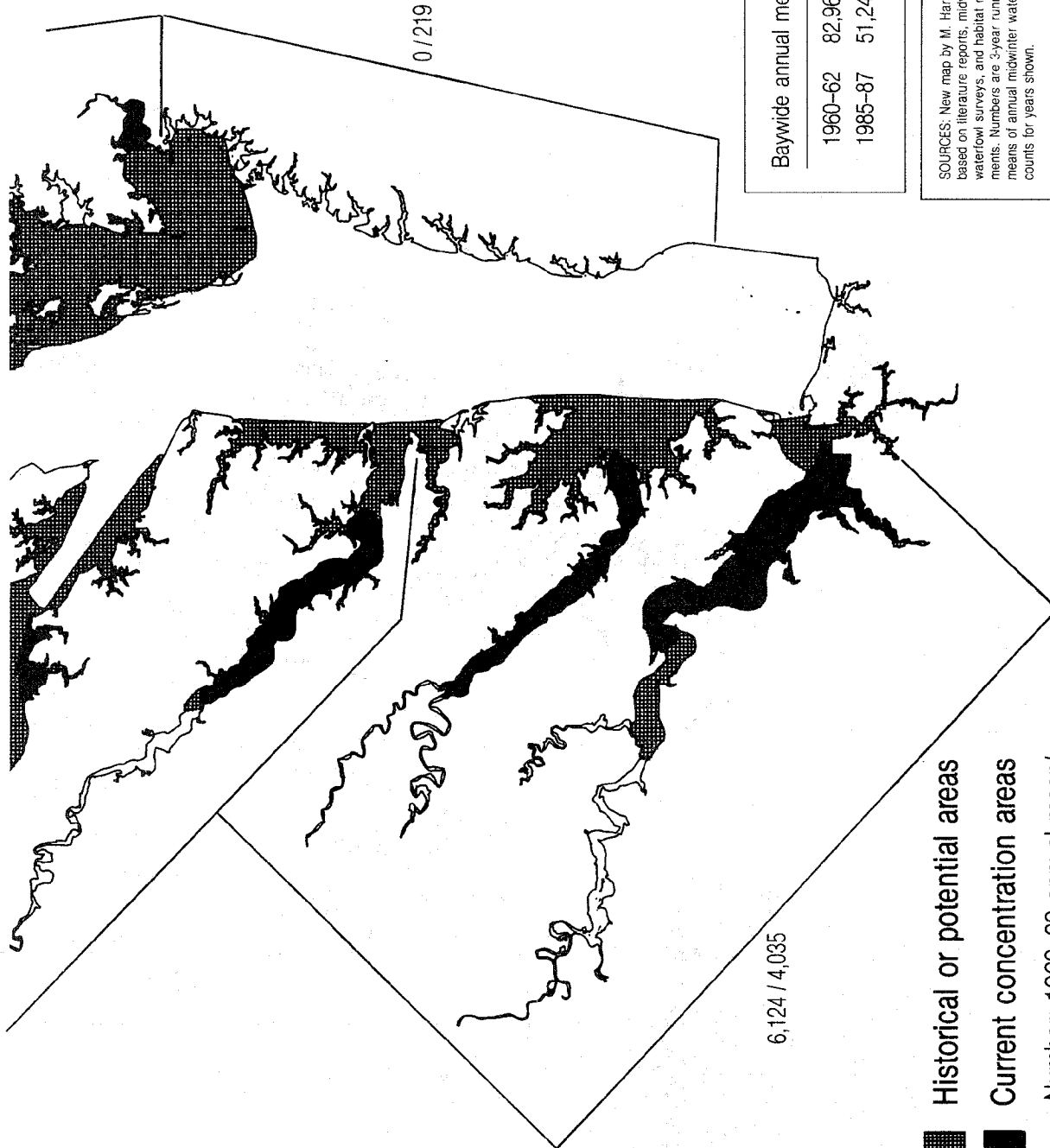
CANVASBACK

Aythya valisineria

Winter Population
Distribution in the
Chesapeake Bay

MAP 37





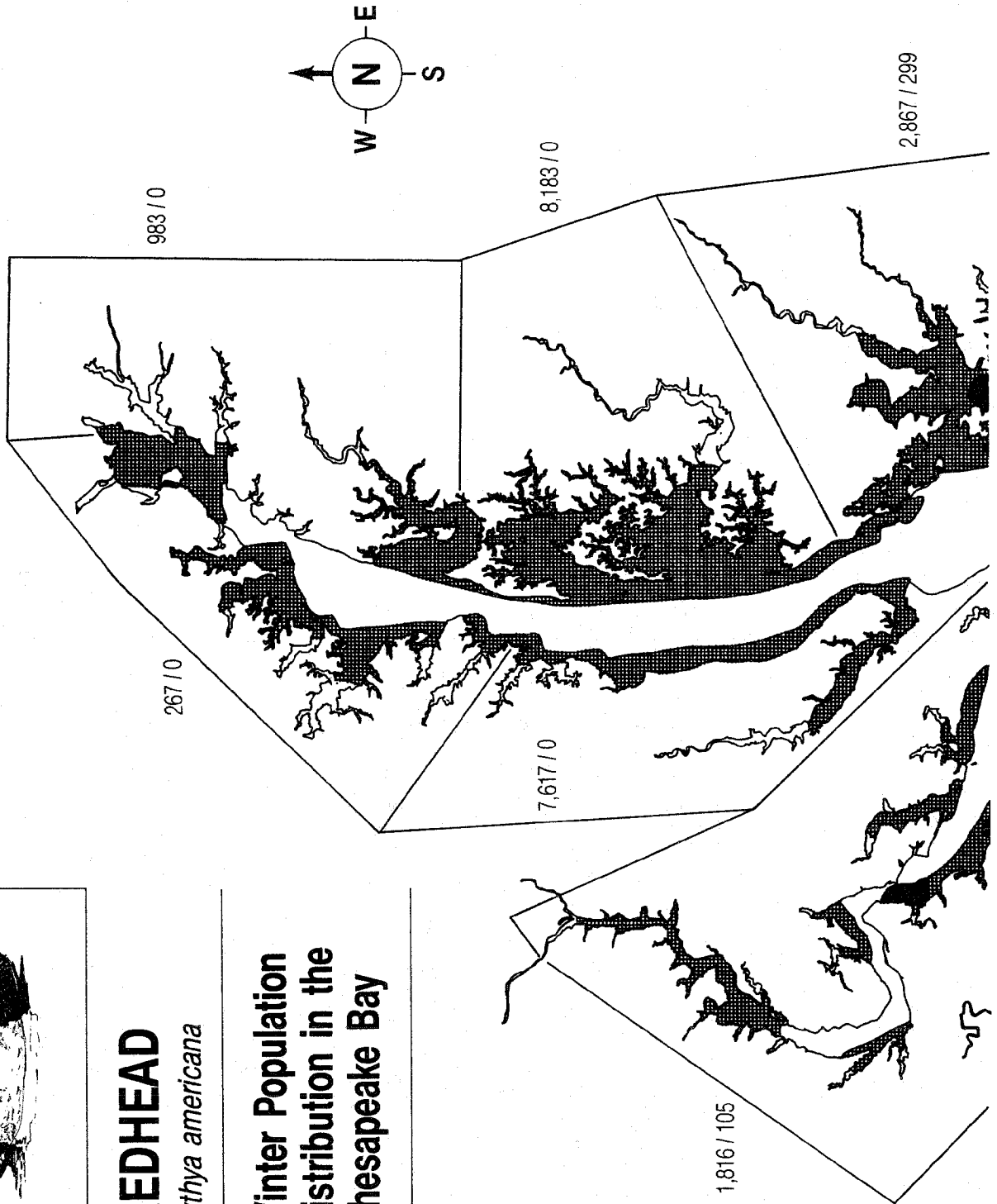


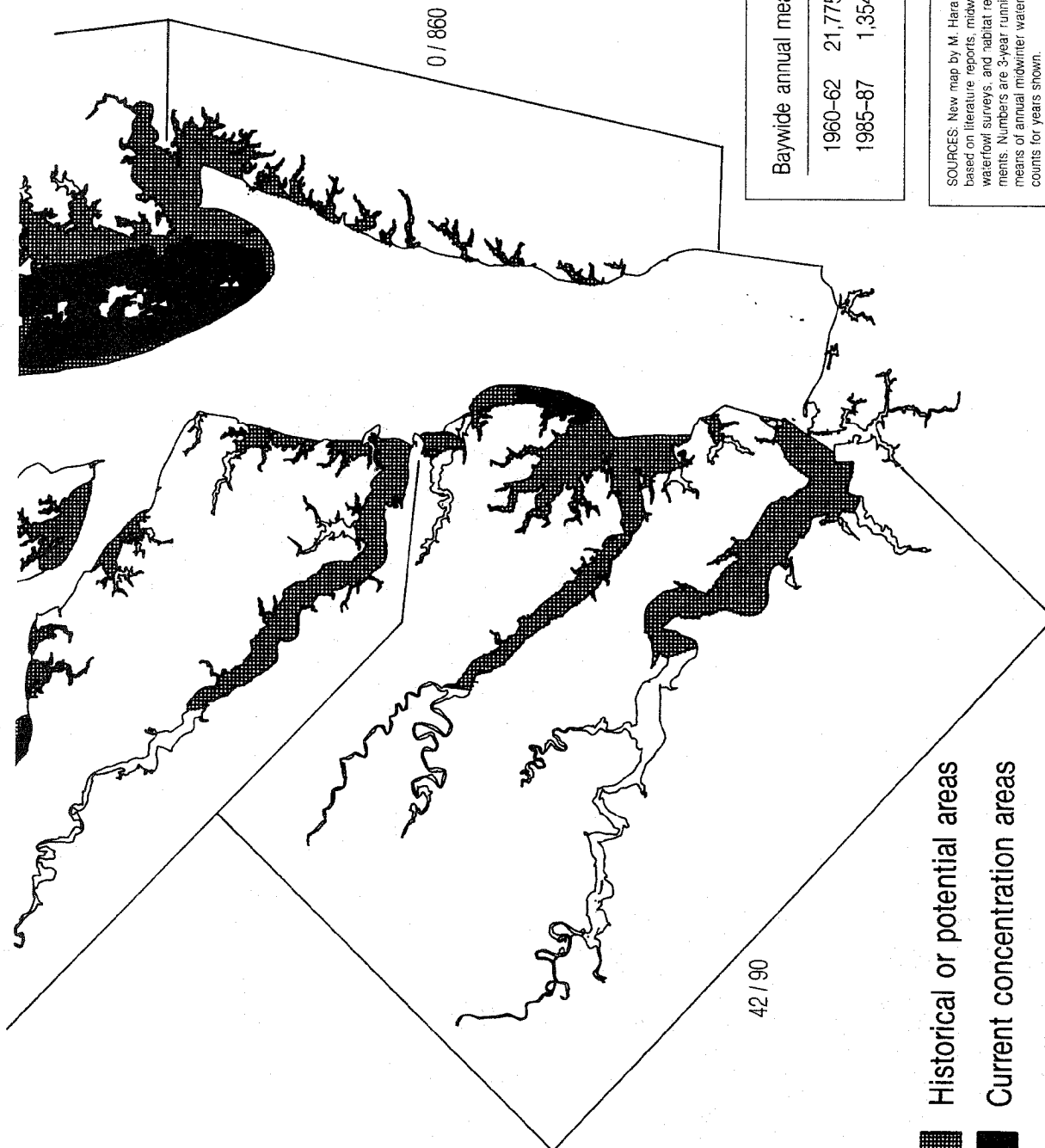
REDHEAD

Aythya americana

Winter Population Distribution in the Chesapeake Bay

MAP 38





Historical or potential areas

Current concentration areas

Numbers: 1960-62 annual mean/
1985-87 annual mean

42 / 90

Baywide annual means

1960-62	21,775
1985-87	1,354

SOURCES: New map by M. Haramis based on literature reports, midwinter waterfowl surveys, and "habitat requirements. Numbers are 3-year running means of annual midwinter waterfowl counts for years shown.

Scale—1:1,069,000

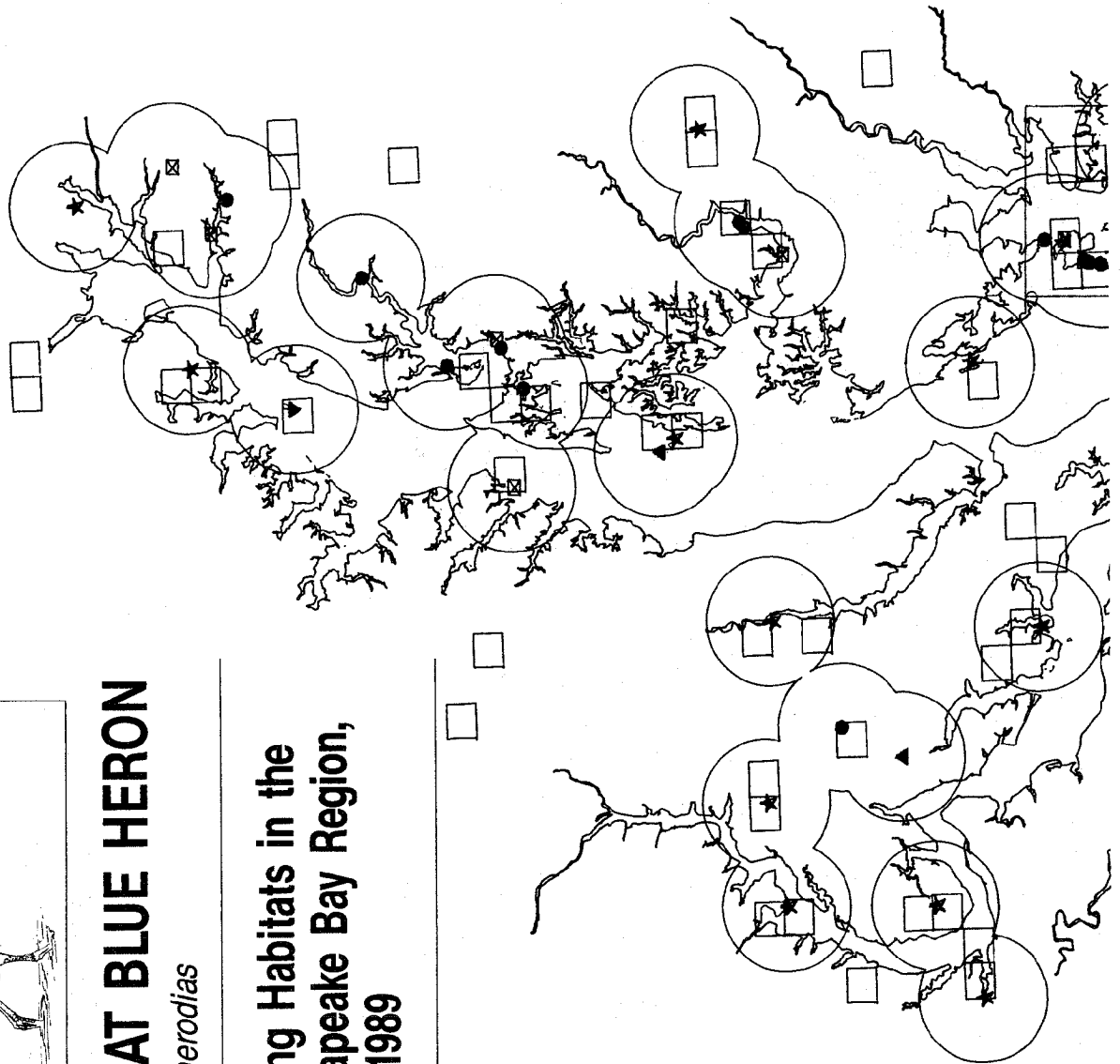
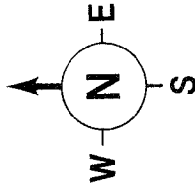


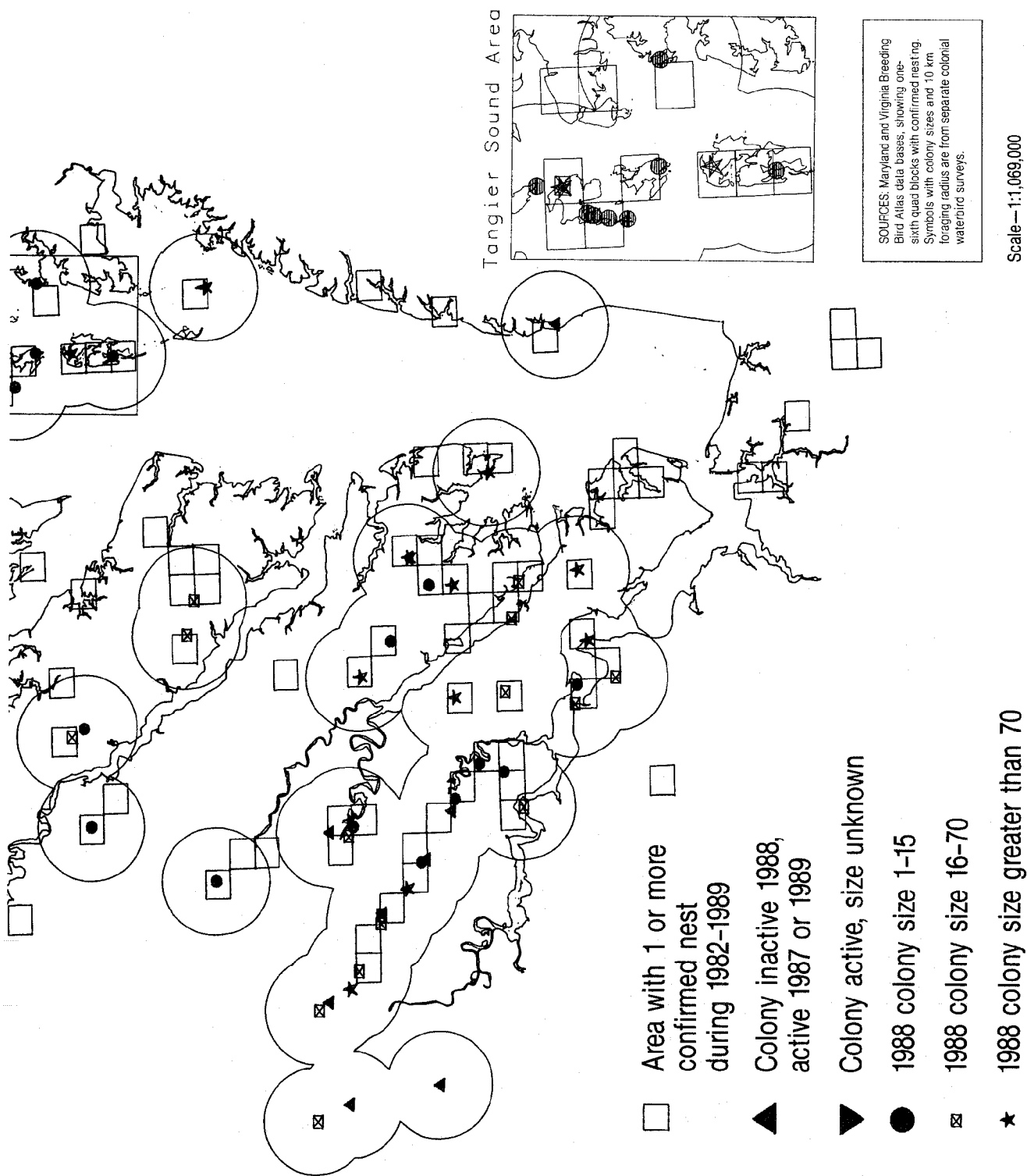
GREAT BLUE HERON

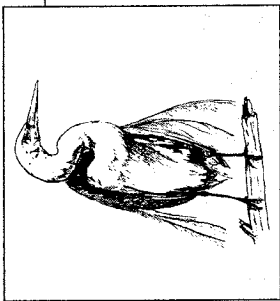
Ardea herodias

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**

MAP 39





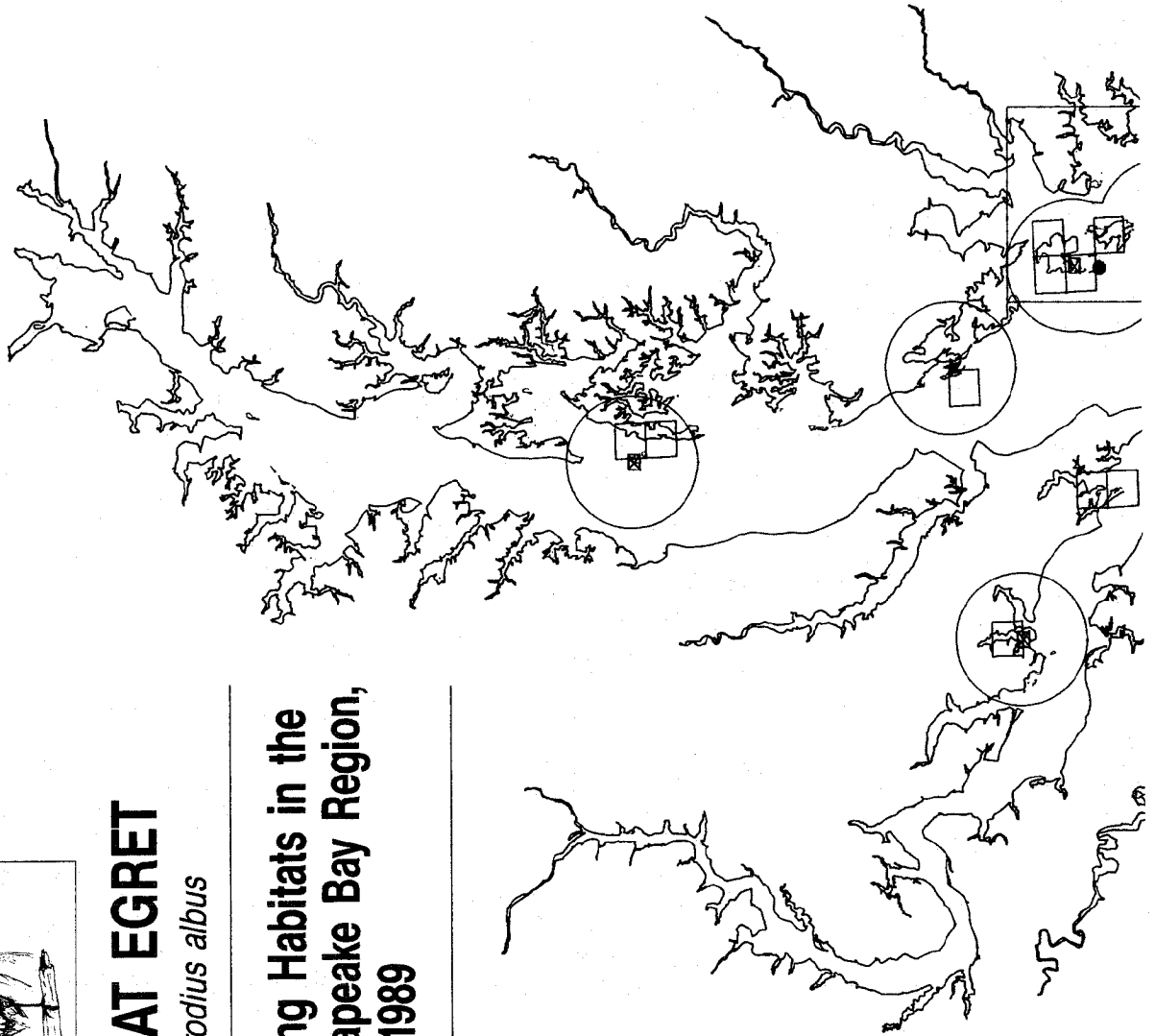
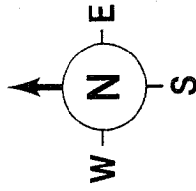


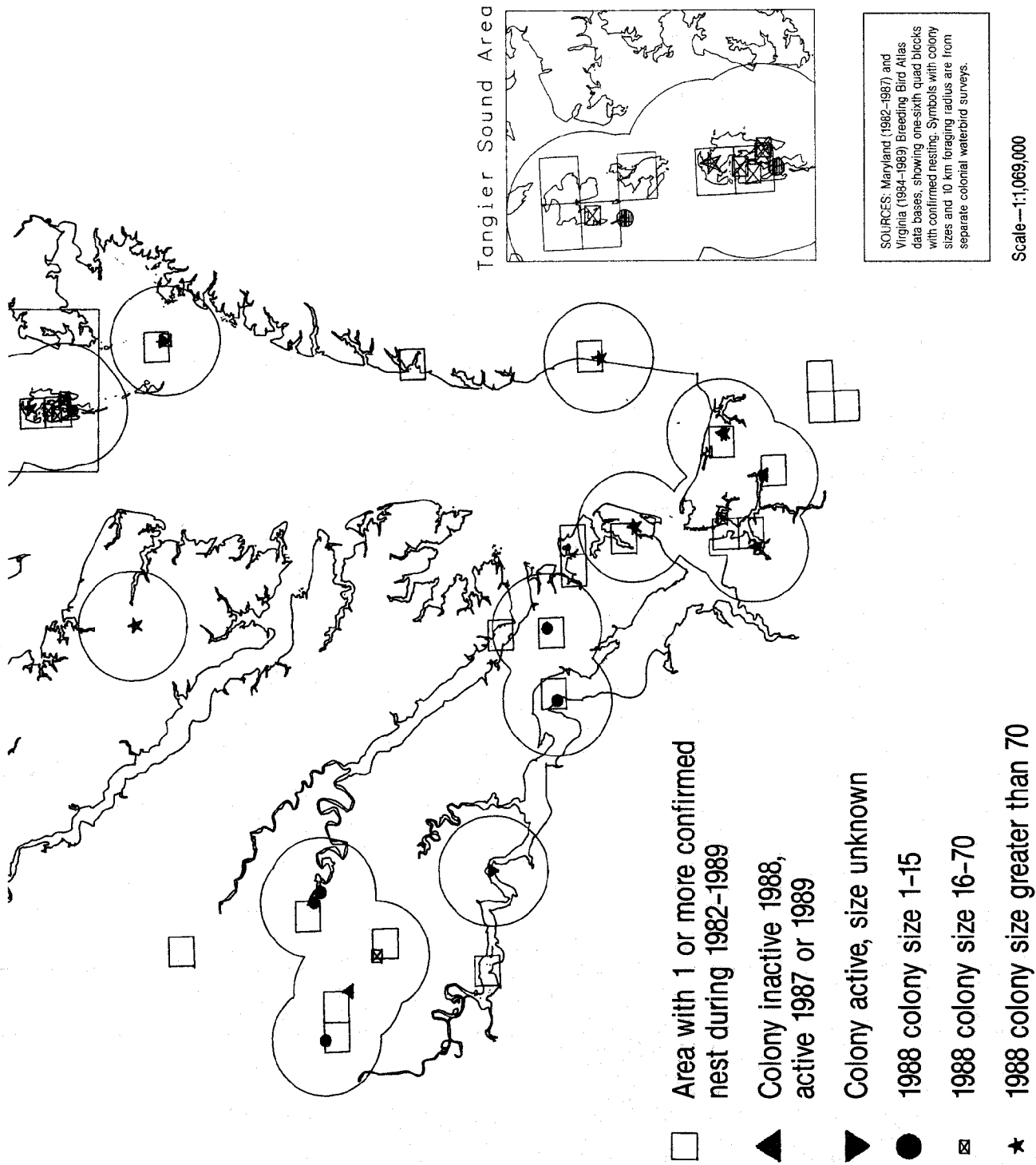
GREAT EGRET

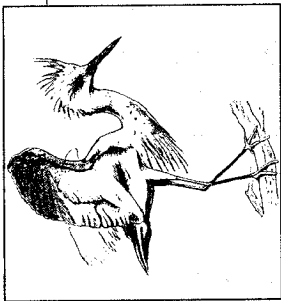
Casmerodius albus

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**

MAP 40





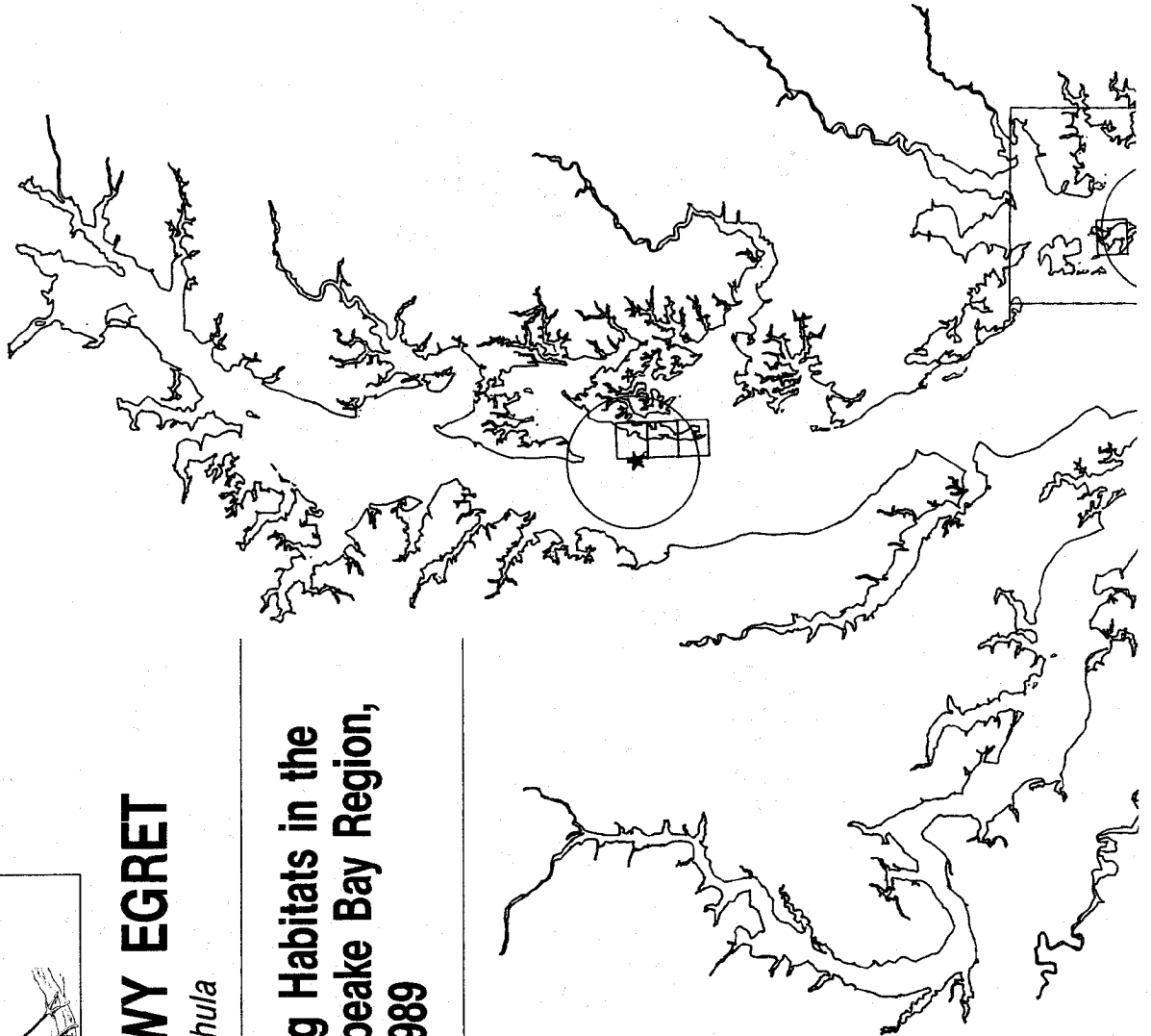
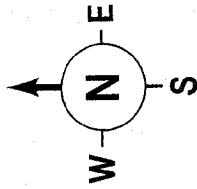


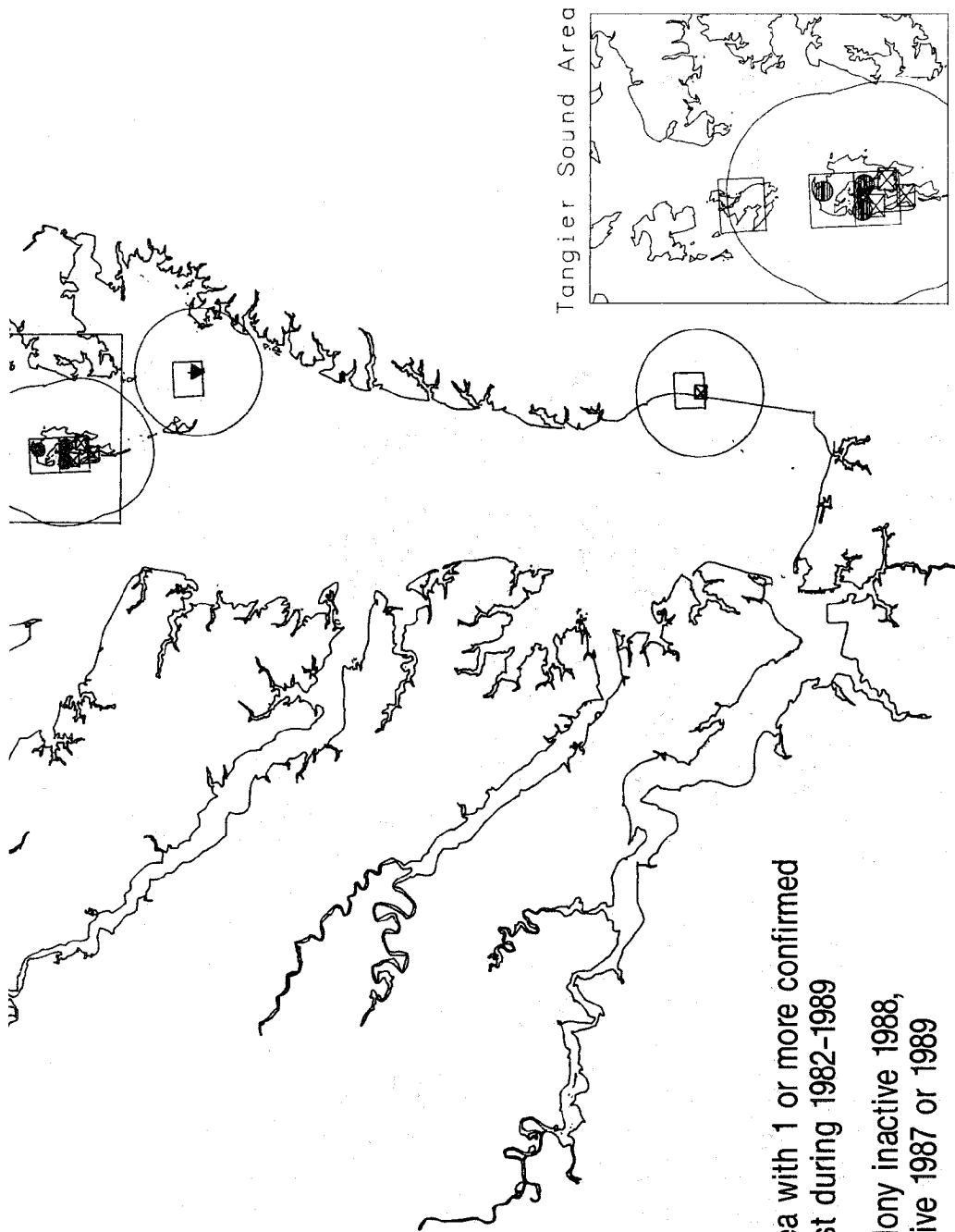
SNOWY EGRET

Egretta thula

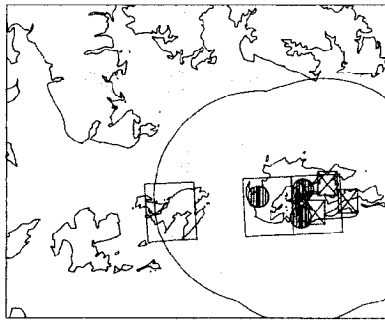
**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**

MAP 41





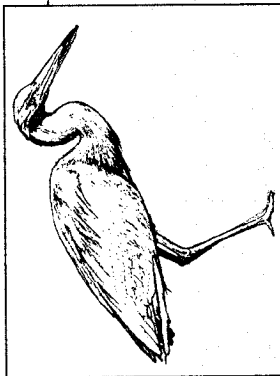
Tangier Sound Area



SOURCES: Maryland (1982-1987) and Virginia (1984-1989) Breeding Bird Atlas data bases, showing one-sixth quad blocks with confirmed nesting. Symbols with colony sizes and 10 km foraging radius are from separate colonial waterbird surveys.

- Area with 1 or more confirmed nest during 1982-1989
- ▲ Colony inactive 1988, active 1987 or 1989
- ▼ Colony active, size unknown
- 1988 colony size 1-15
- ▣ 1988 colony size 16-70
- ★ 1988 colony size greater than 70

Scale—1:1,069,000

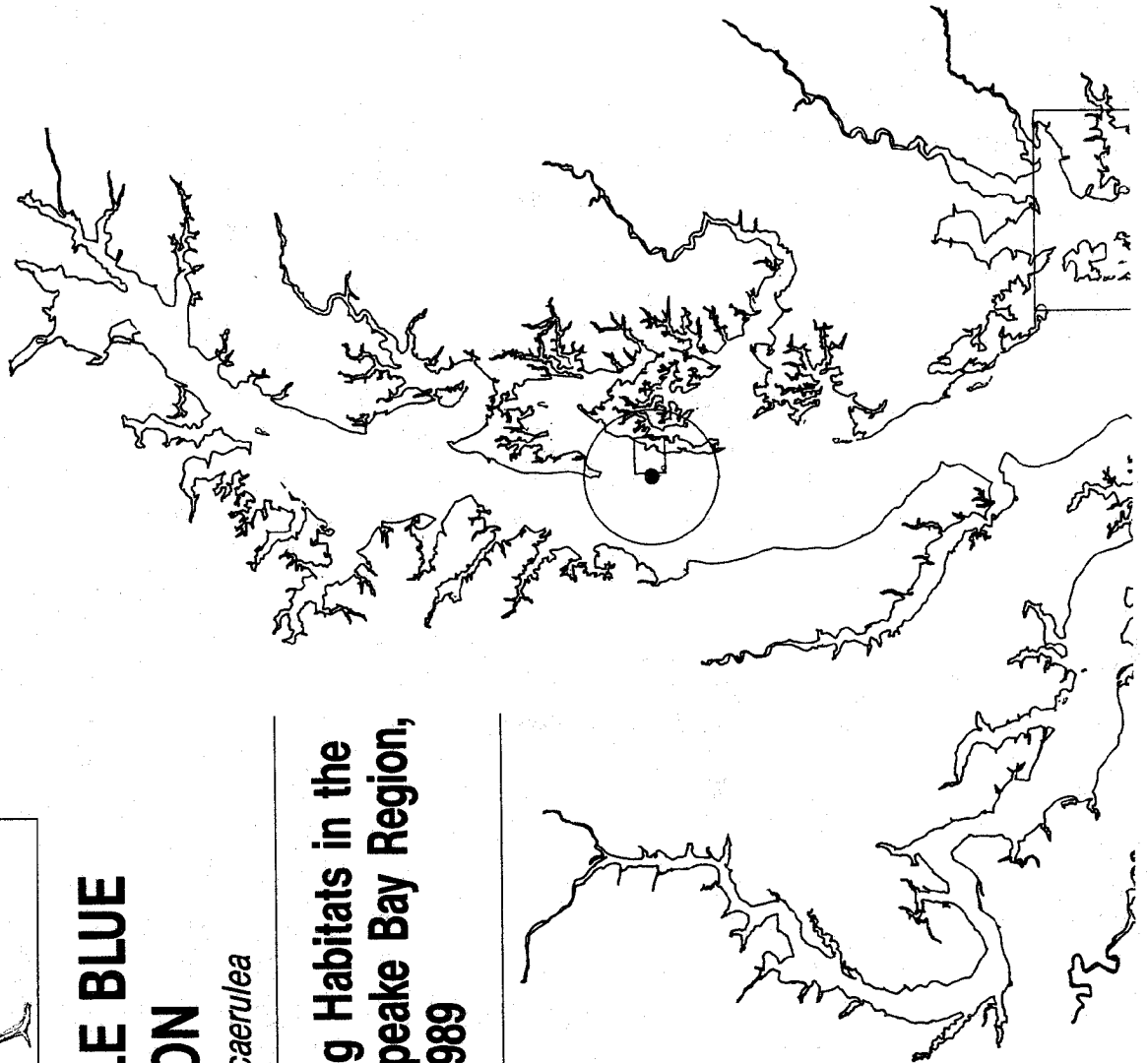
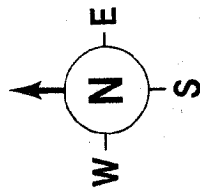


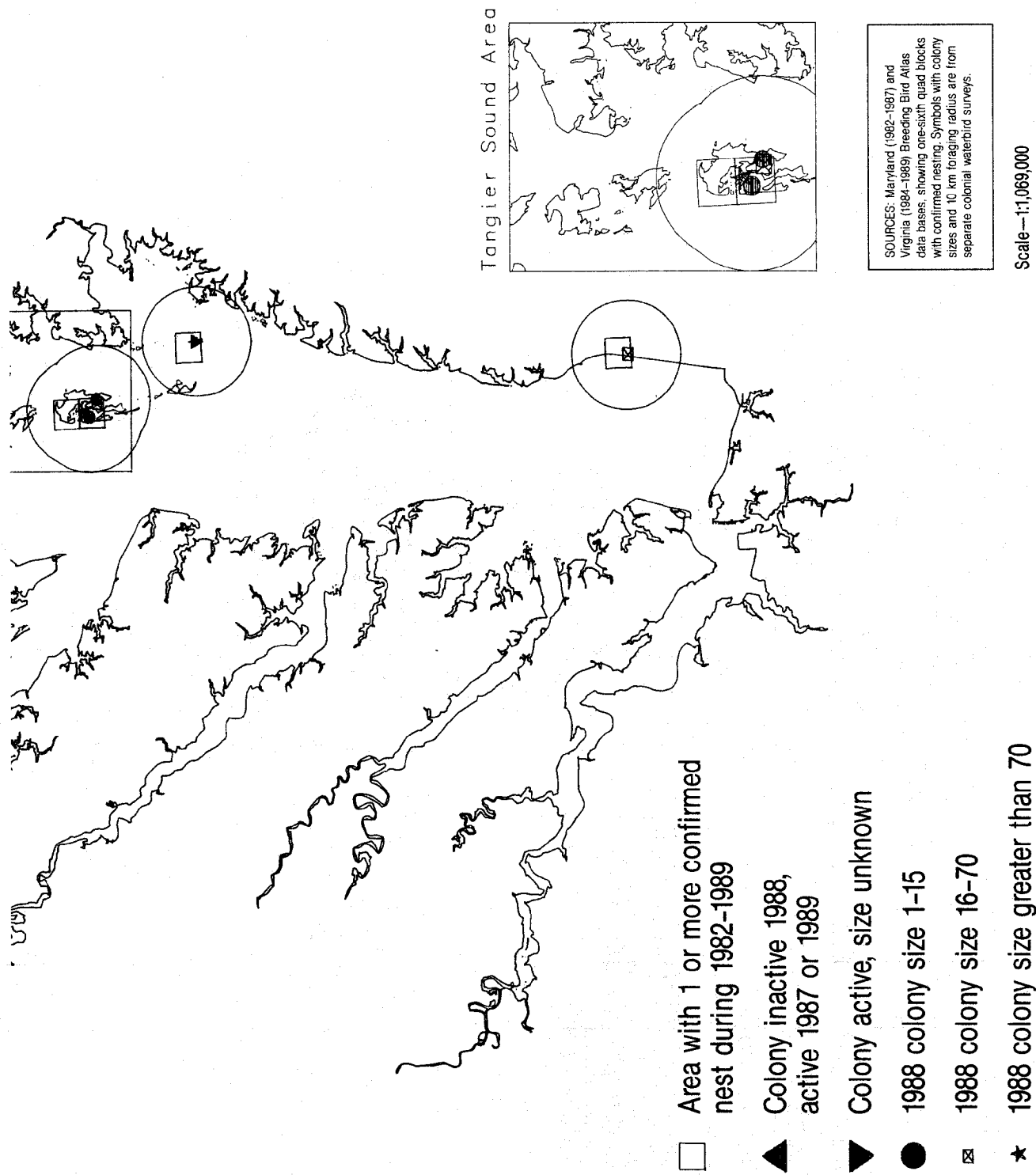
LITTLE BLUE HERON

Egretta caerulea

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**

MAP 42





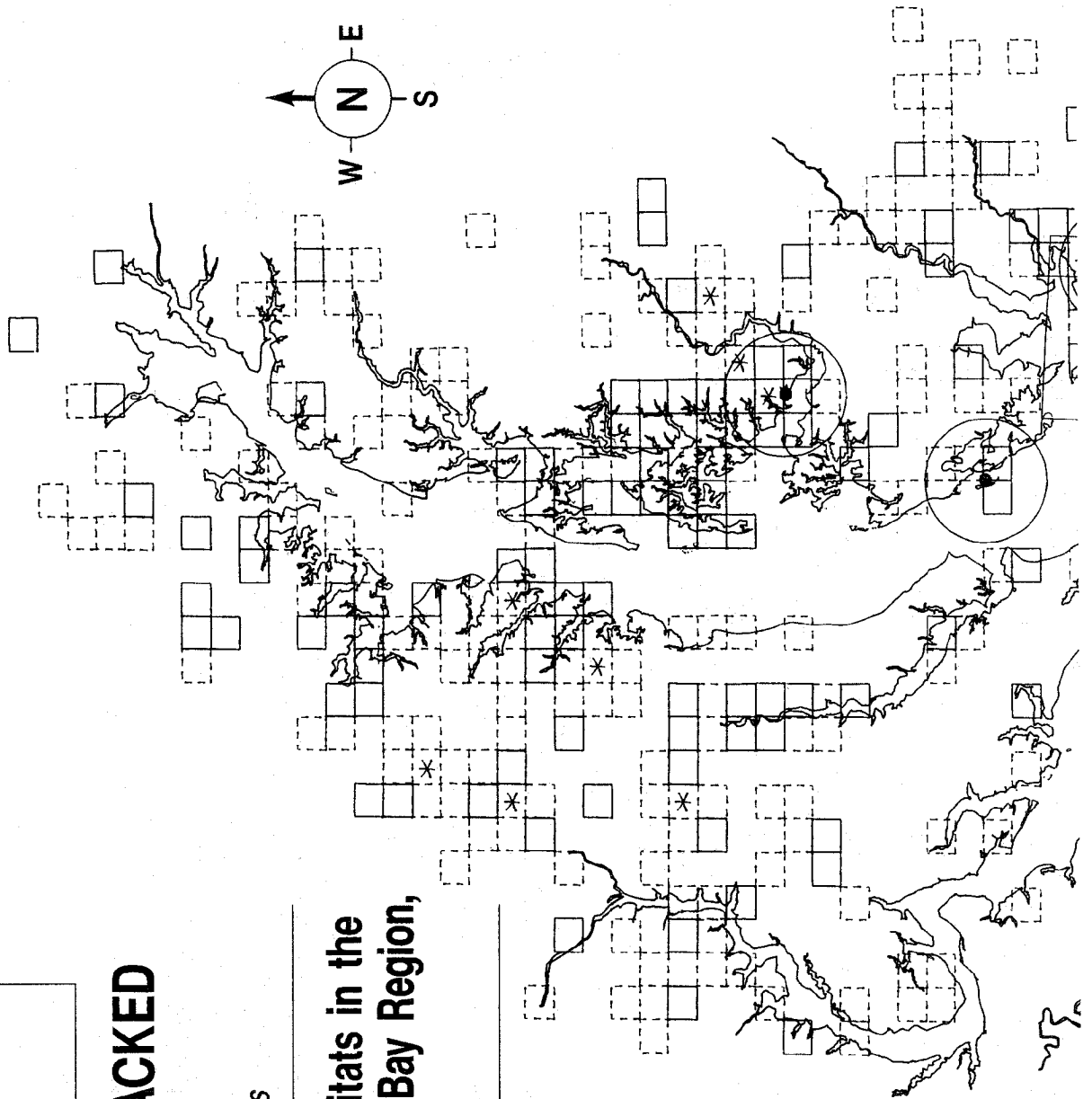


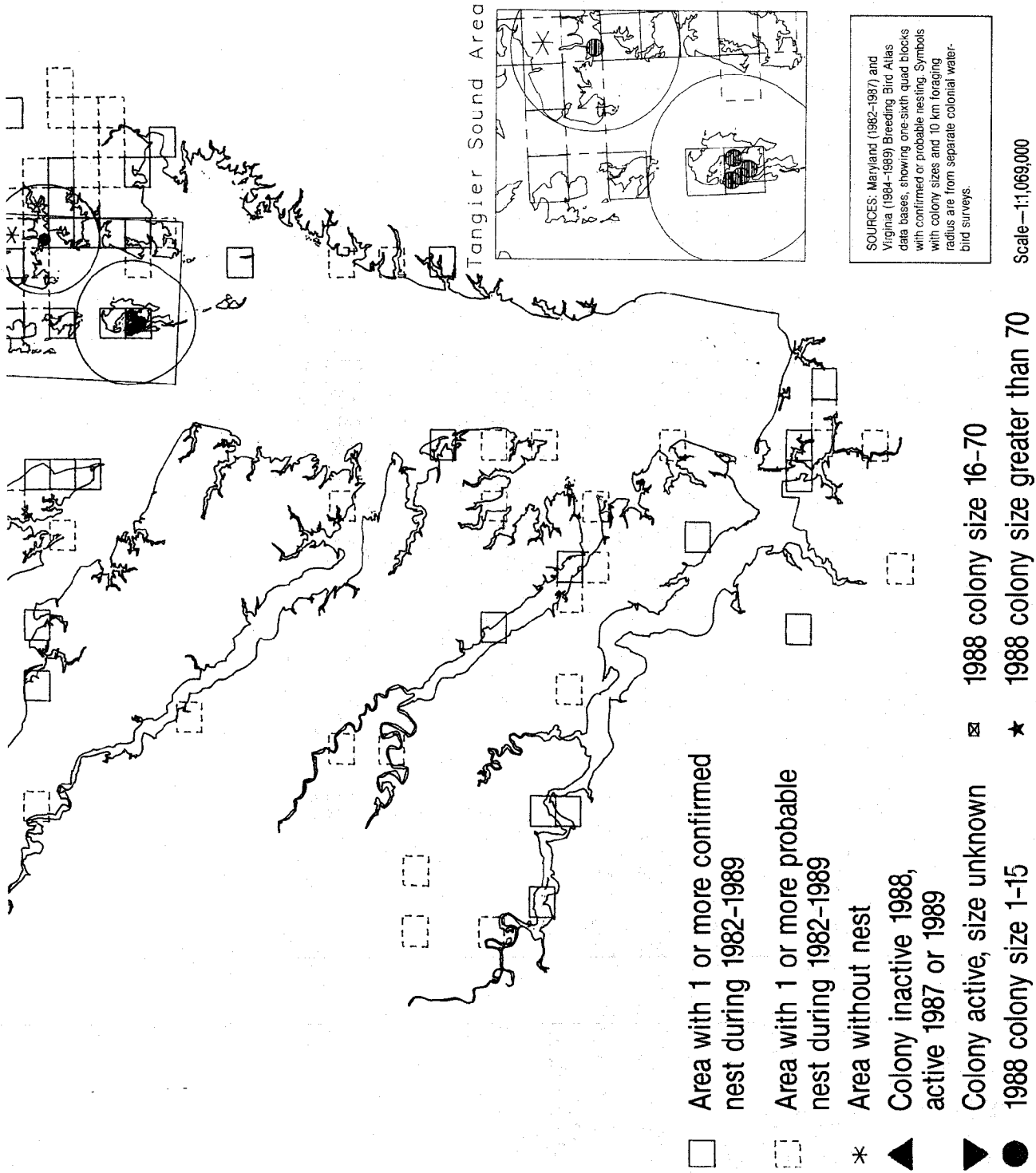
GREEN-BACKED HERON

Butorides striatus

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**

MAP 43





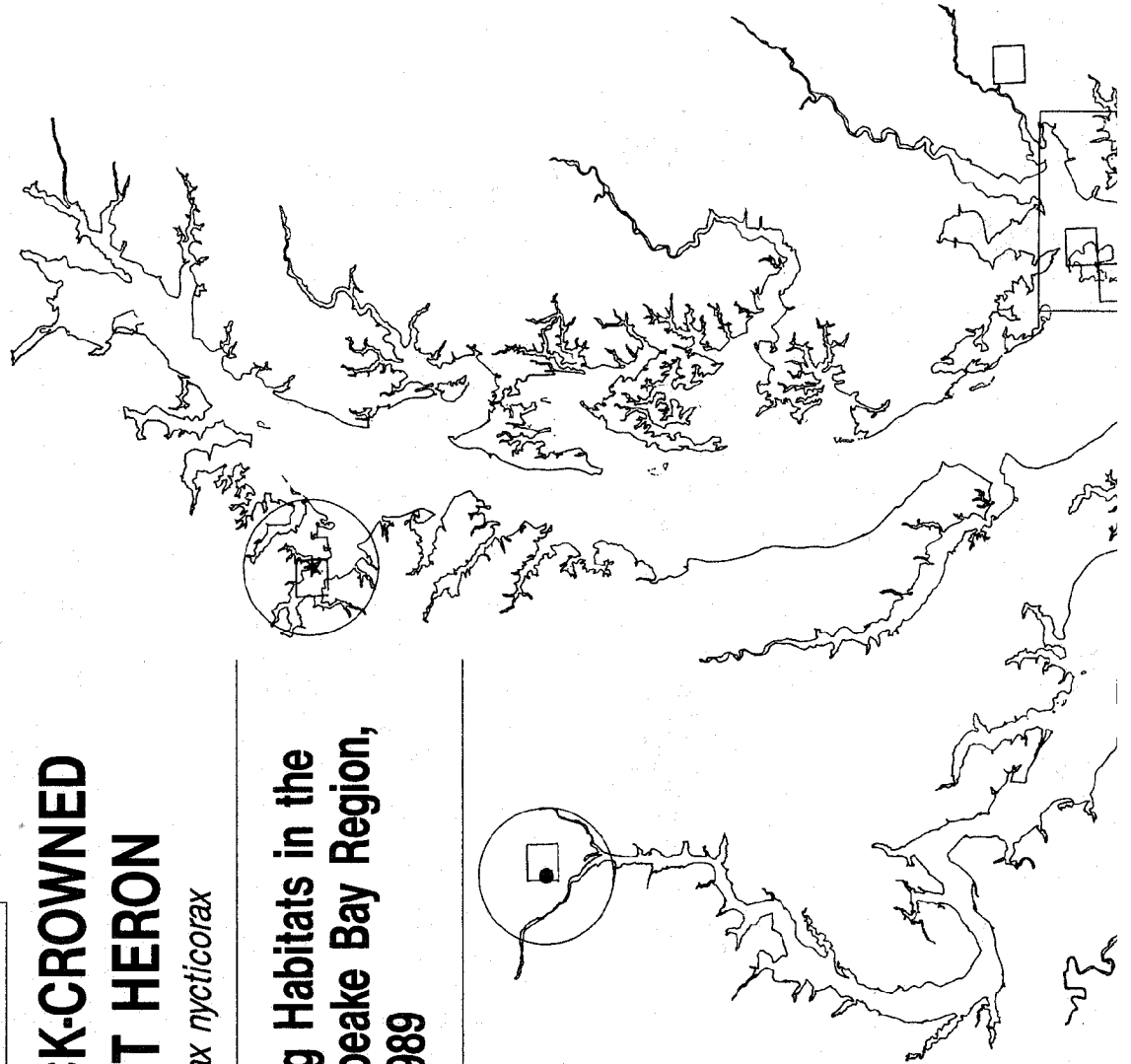
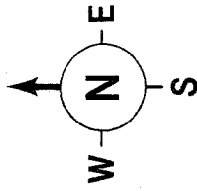


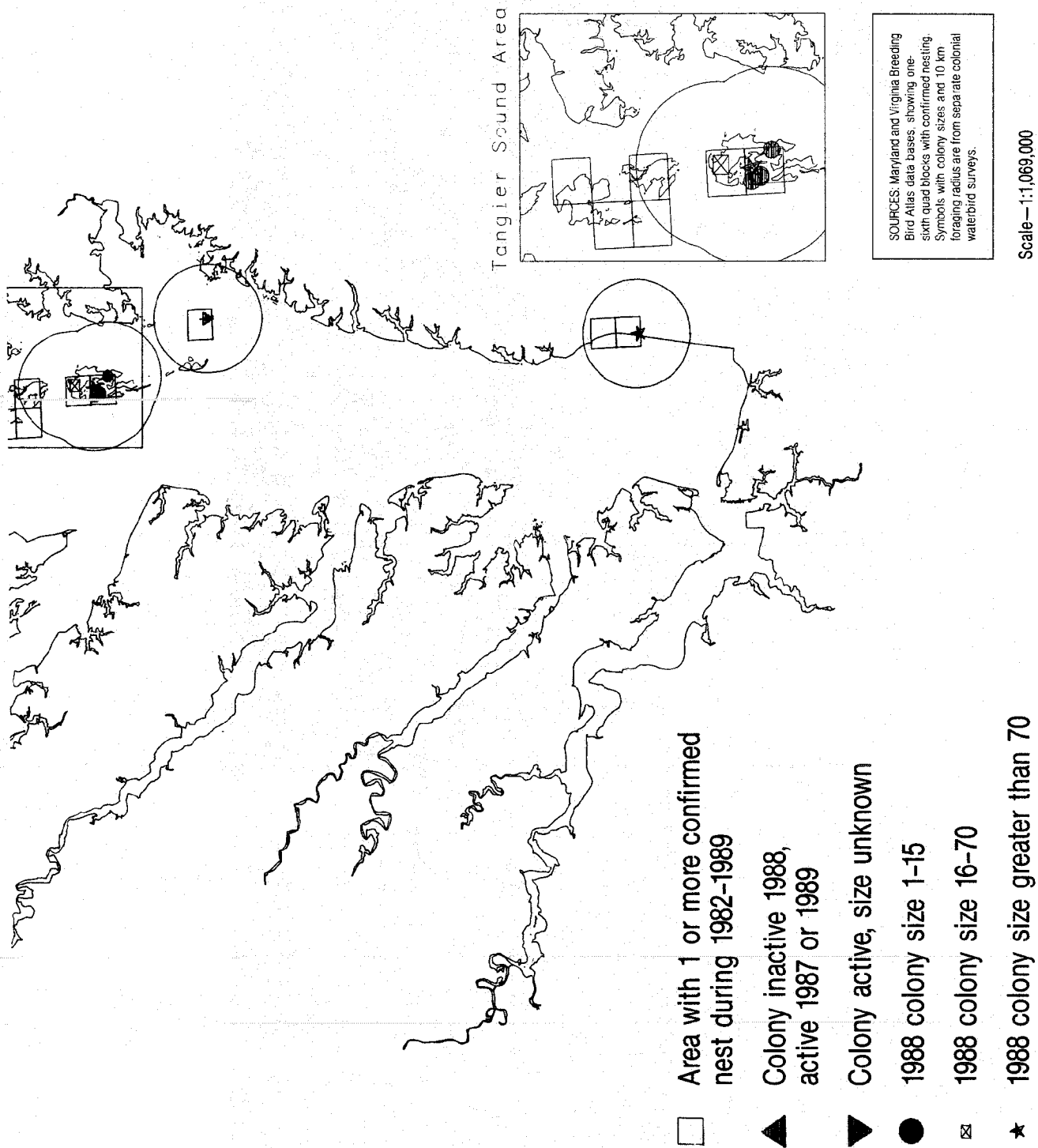
MAP 44

BLACK-CROWNED NIGHT HERON

Nycticorax nycticorax

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**



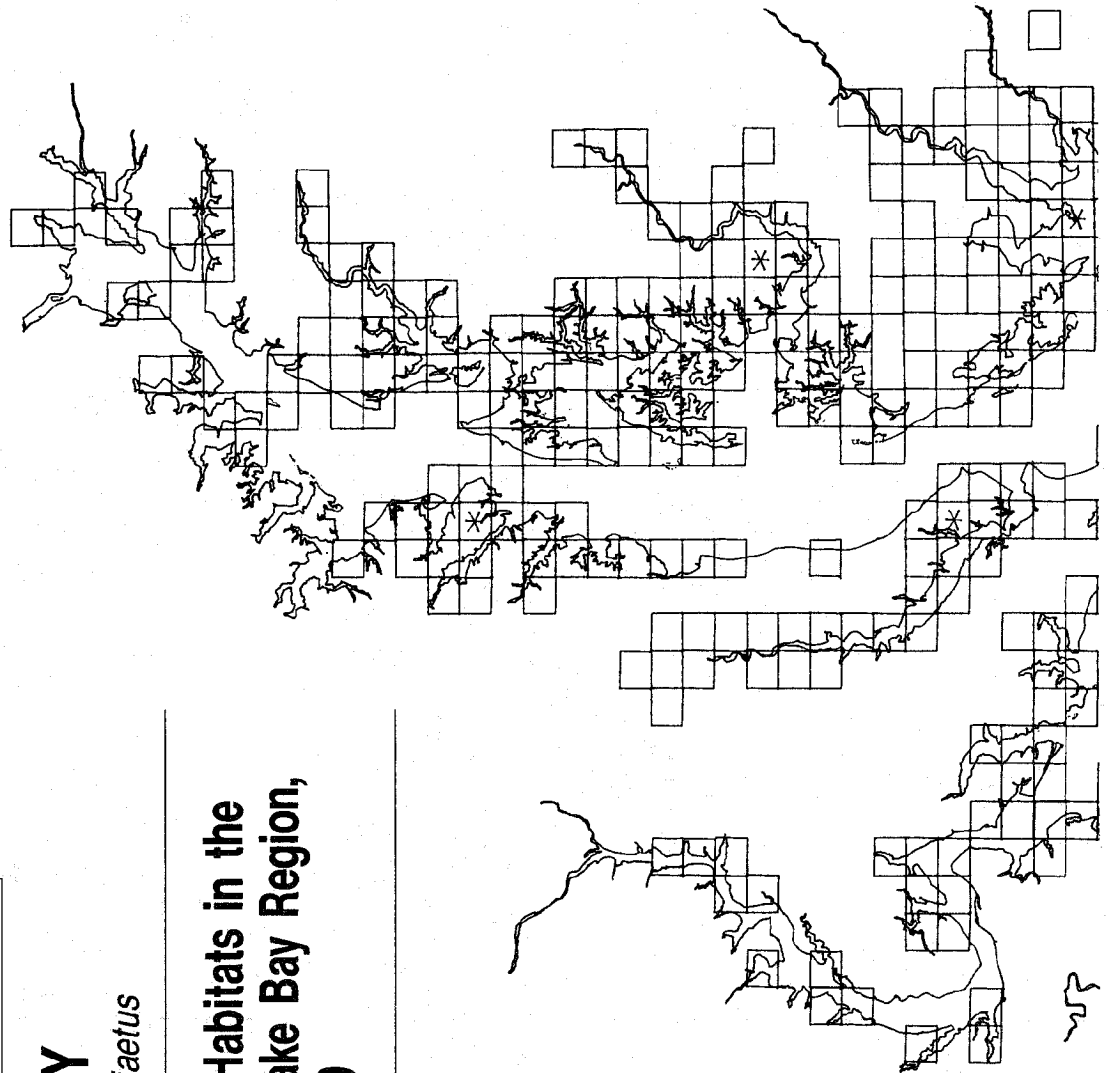
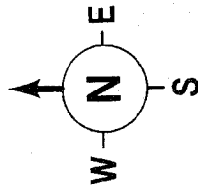


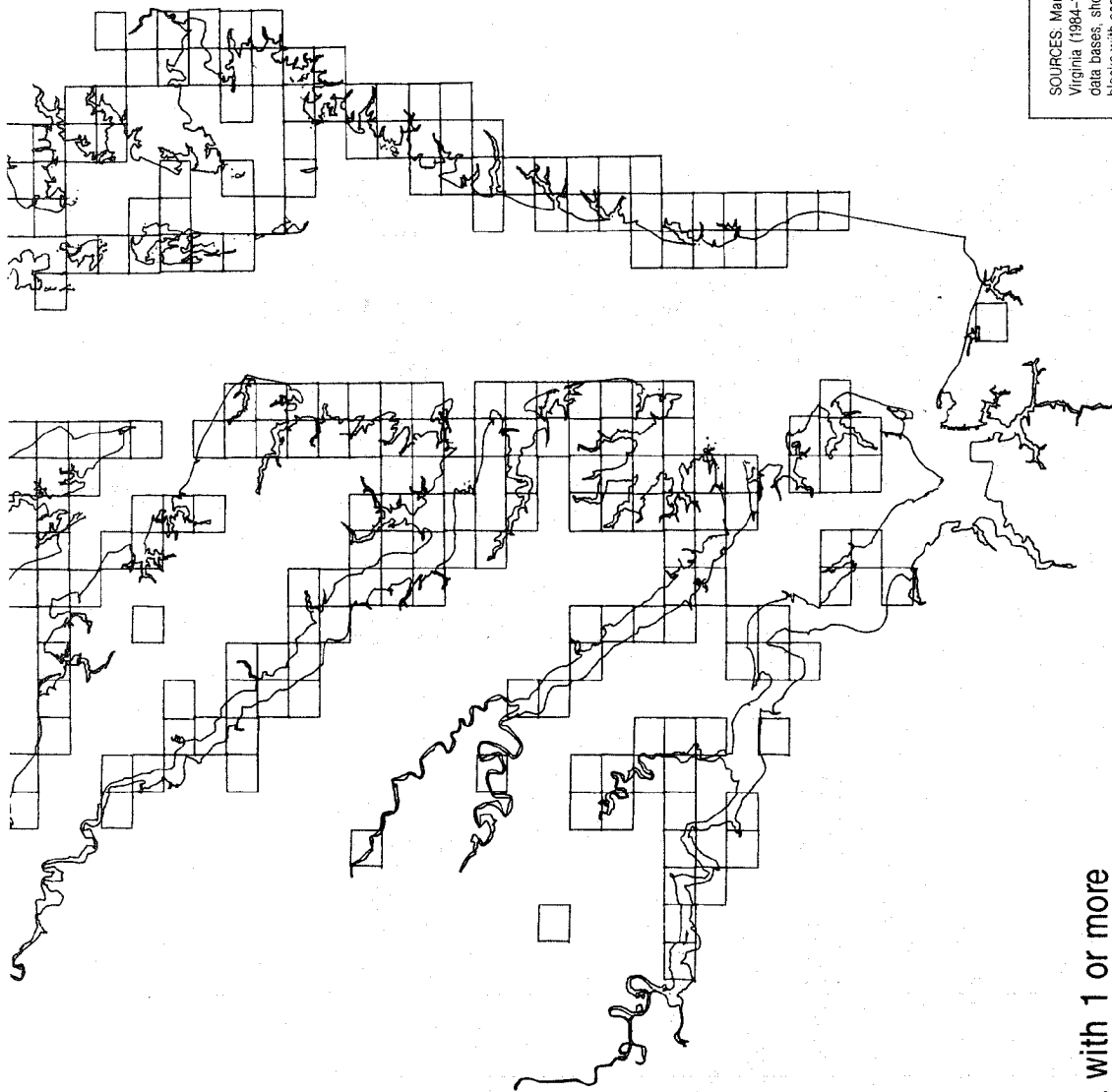


MAP 45

OSPREY *Pandion haliaetus*

**Nesting Habitats in the
Chesapeake Bay Region,
1982-1989**



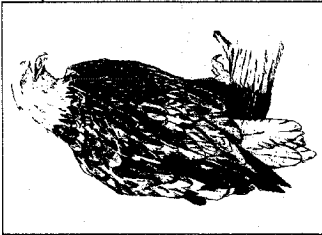


☐ Area with 1 or more confirmed nest during 1982-1989

☐ * Area without nest

SOURCES: Maryland (1982-1990) and Virginia (1984-1989) Breeding Bird Atlas data bases, showing one-sixth quad blocks with confirmed nesting. Additional Maryland data from G. Therres. Blocks with asterisks did not have nests, but appeared to because adjoining areas had nests.

Scale—1:1,069,000

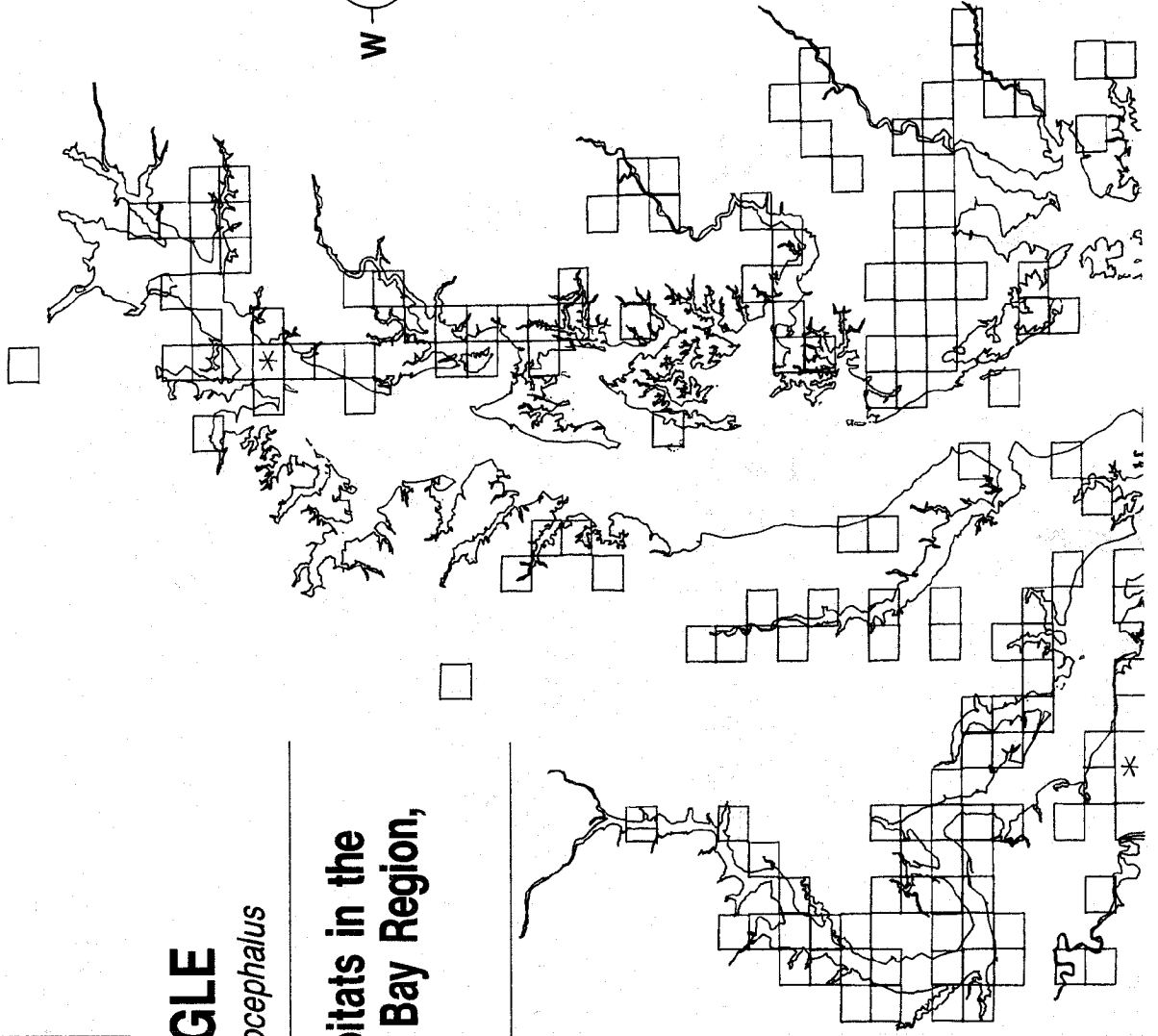
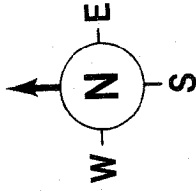


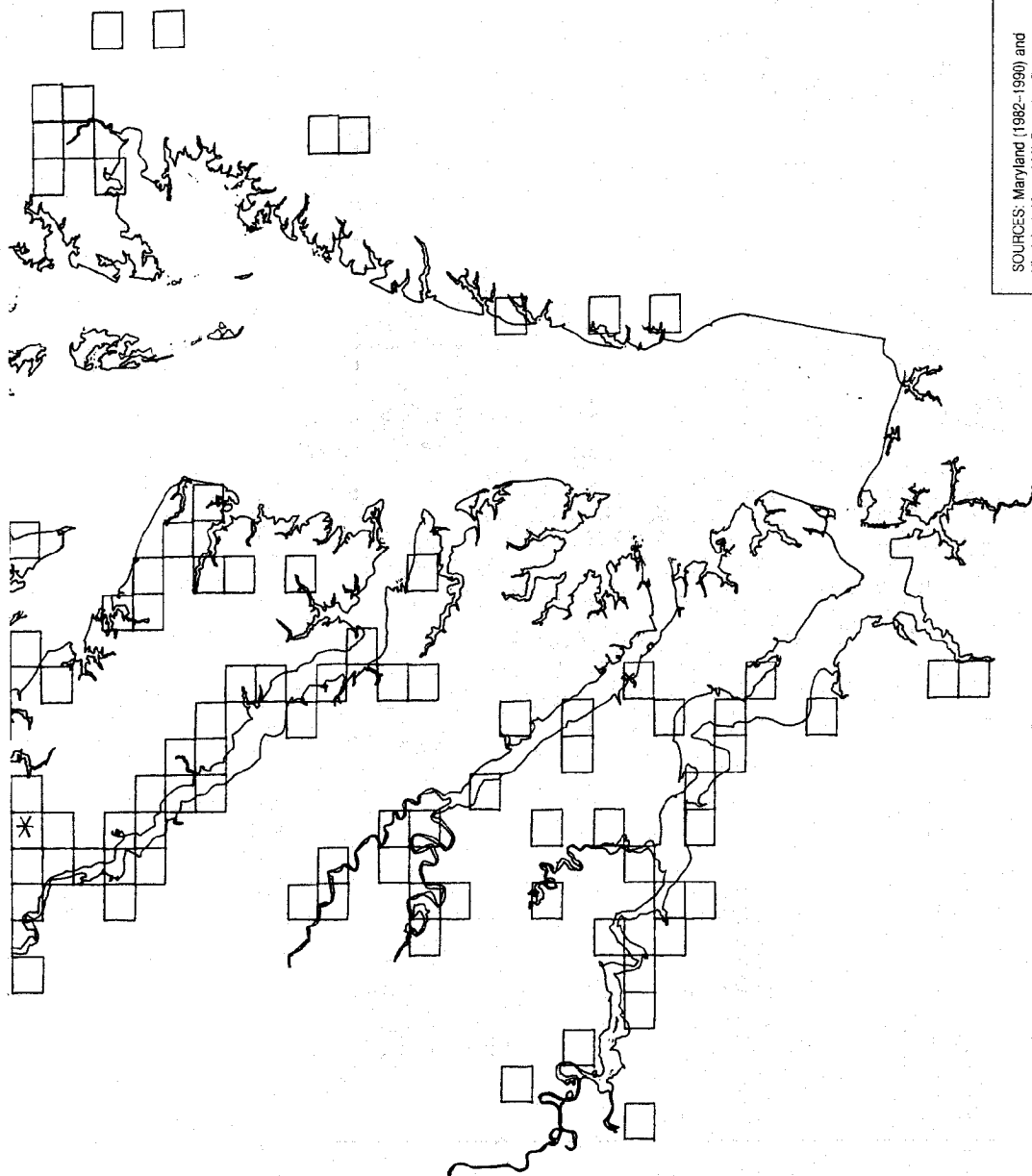
BALD EAGLE

Haliaeetus leucocephalus

Nesting Habitats in the
Chesapeake Bay Region,
1982-1990

MAP 46



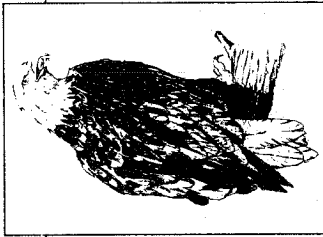


SOURCES: Maryland (1982-1990) and Virginia (1984-1989) Breeding Bird Atlas data bases, showing one-sixth quad blocks with confirmed nesting. Additional Maryland data from G. Therres. Blocks with asterisks did not have nests, but appeared to because adjoining areas had nests.

Scale—1:1,069,000

□ Area with 1 or more confirmed nest during 1982-1990

* Area without nest

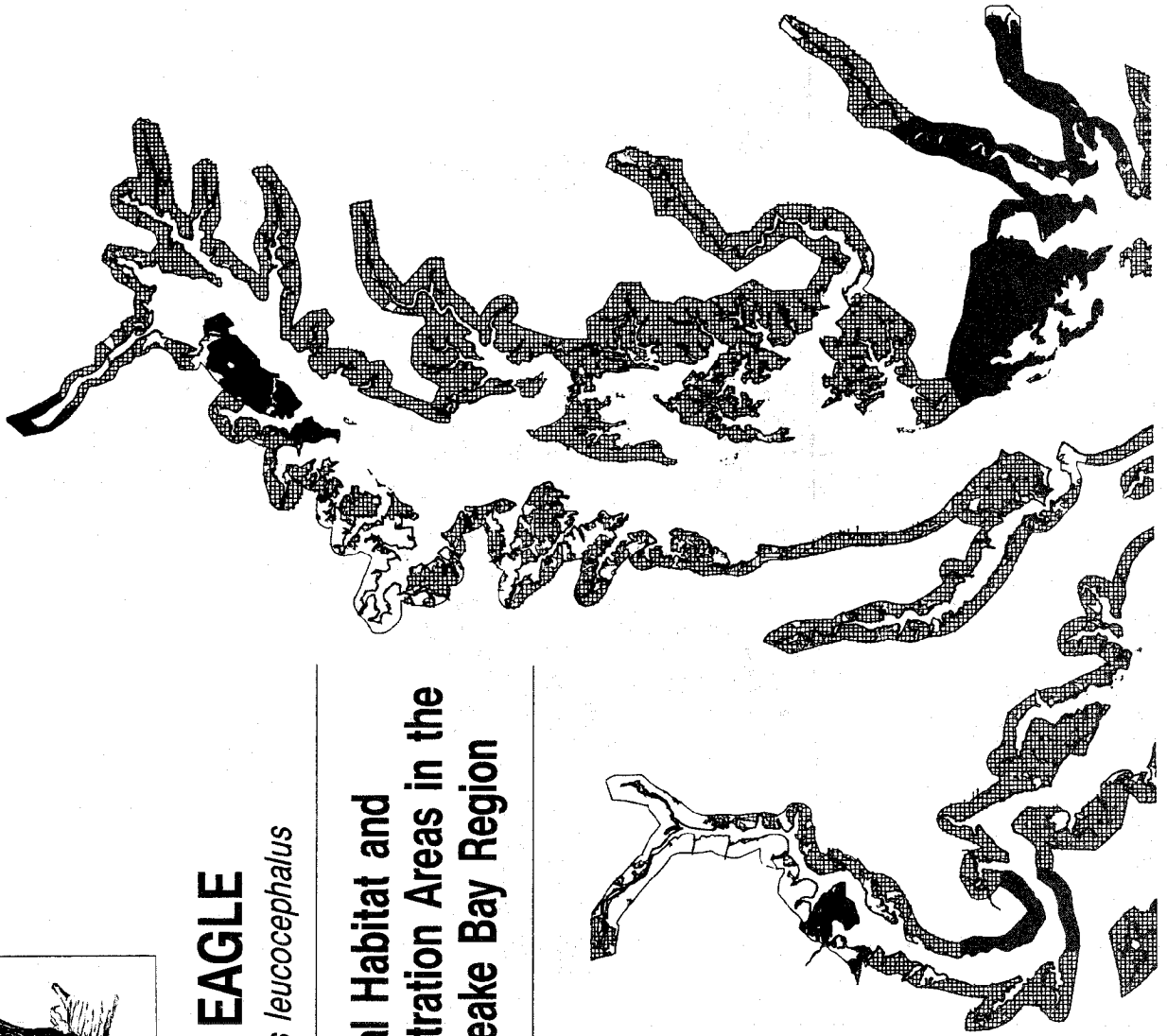
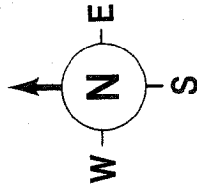


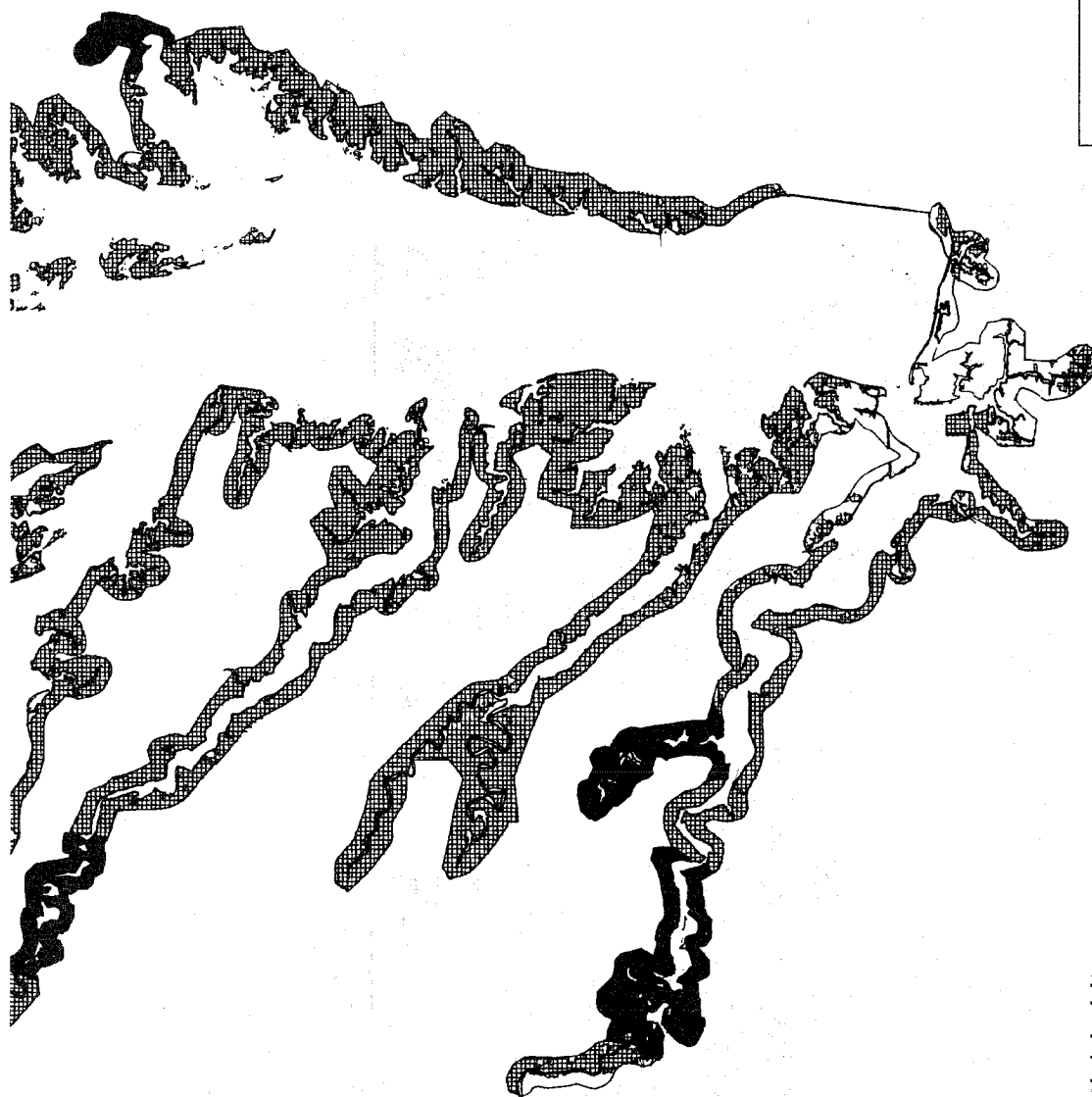
MAP 47

BALD EAGLE

Haliaeetus leucocephalus

Potential Habitat and
Concentration Areas in the
Chesapeake Bay Region





SOURCES: Potential is a 2 km wide shoreline buffer, minus any areas of urban land use as defined by USGS. Concentration areas were delineated by J. Fraser based on survey data, and include all seasons.

- Potential habitat
- Concentration areas
- Excluded urban areas

Scale—1:1,069,000

